JOURNAL
OF THE
ARNOLD ARBORETUM

VOLUME 64 | APRIL 1983 | NUMBER 2

SYSTEMATICS OF THE ANDROPOGON VIRGINICUS COMPLEX (GRAMINEAE)

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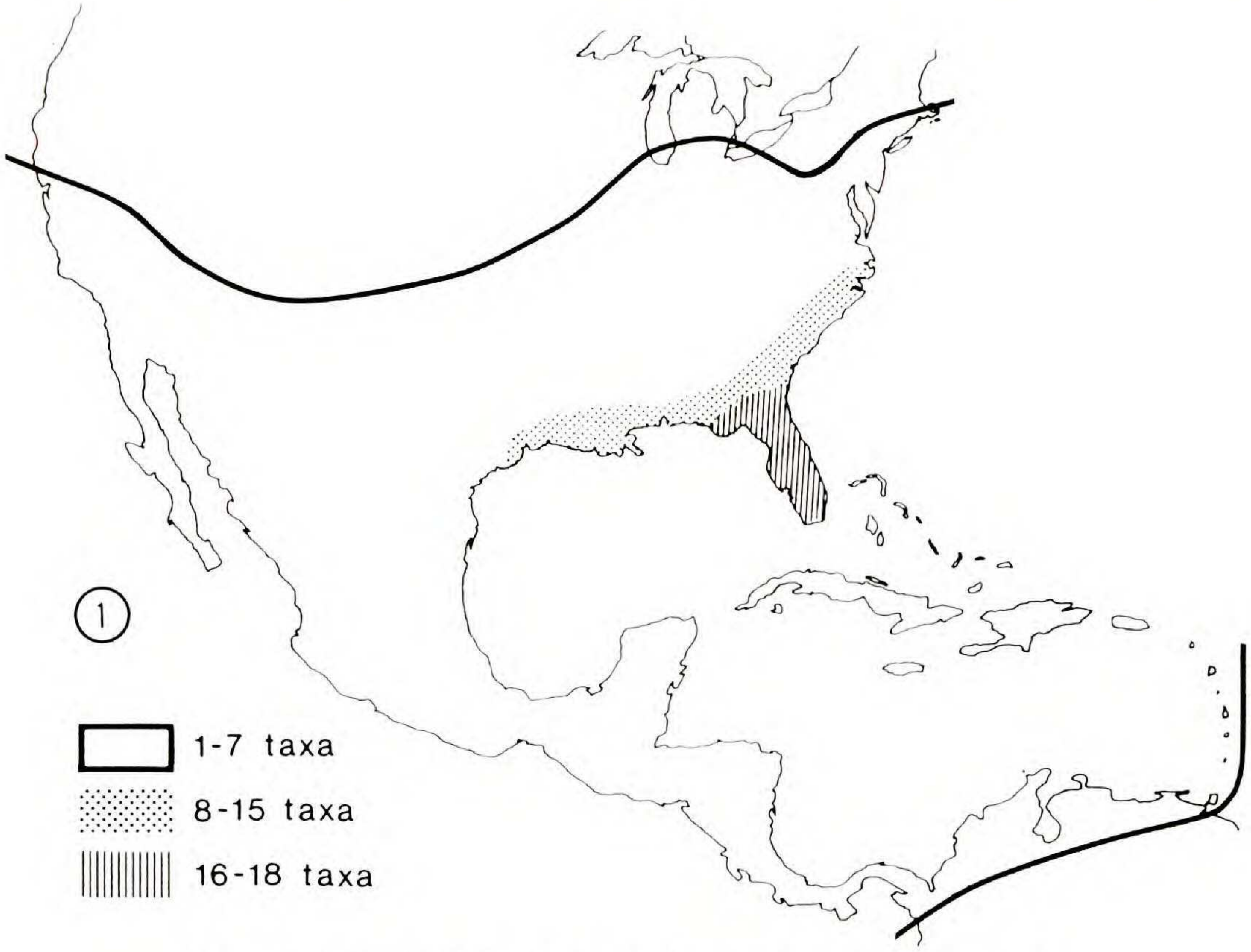
THE ANDROPOGON VIRGINICUS COMPLEX is a closely interrelated group of nine species that range over much of the northern half of the New World (MAP 1). These grasses are weedy, diploid, sexual, cespitose perennials. The taxonomy of the broomsedges, as they are commonly called, has been confounded by the paucity and subtlety of taxonomically useful morphological characters and by the strong similarity of many of the taxa. Moreover, chromosome number and flavonoid chemistry have not provided additional usable variation. In this study, taxonomic rank is therefore based on morphological distance, supported by ecological and geographic differences. On the basis of extensive field observations and laboratory and herbarium study of the plants, twenty taxa are recognized. Four of the nine species include two or more varieties, and four of these varieties contain nine taxa, here called variants, that are not sufficiently distinct morphologically to warrant formal nomenclatural status. These variants have been given English names describing some aspect of their morphology, ecology, geography, or general nature. Six of the variants correspond to previously described taxa, and three are discussed here for the first time.

The center of diversity of the group, both for number of taxa and abundance of individual plants, is the Coastal Plain of the southeastern United States. The combination of effective wind dispersal of the fruit, frequent inbreeding, and relative competitive superiority makes the plants of the virginicus complex successful colonizers under conditions of density-independent mortality. Many of the taxa rapidly form large, dense populations wherever there is full sun and in all but the poorest and driest of soils. *Andropogon virginicus* L. var. *virginicus* dominates all other vegetation in the early stages of old-field succession in much of the eastern United States (Keever, 1950; Golley, 1965; Bazzaz, 1975). Like many other inbreeding, colonizing groups, the virginicus complex contains numerous taxa that are very similar morphologically (Stebbins, 1957; Lelong, 1965; Kannenberg & Allard, 1967).

These very similar taxa frequently grow together but rarely produce apparent

Journal of the Arnold Arboretum **64:** 171–254. April, 1983.



MAP 1. Distribution of the *Andropogon virginicus* complex.

hybrids (Campbell, 1980). They are effectively reproductively isolated from one another without being separated by large morphological gaps. These sibling species have been a taxonomic problem because, although they represent discrete variation, they are very difficult to distinguish. All of them belong to the three most widespread and weedy species, *Andropogon gyrans, A. virginicus,* and *A. glomeratus.* It is not surprising that authors of previous treatments of these species do not agree on the number of taxa that should be recognized (TABLE 1). Nash (1903) and Hitchcock (1951) overdescribed these species, and Roberty (1960), Radford *et al.* (1964), and Long and Lakela (1971) did not describe the variation sufficiently. Hackel (1889) and Fernald and Griscom (1935) misinterpreted some of the relationships within the virginicus complex, but the treatments by these authors provide the most insightful contributions to an understanding of the taxonomy of the group.

TAXONOMIC POSITION AND DEFINITION OF THE VIRGINICUS COMPLEX

The Linnaean concept of the genus *Andropogon* corresponds roughly to the current circumscription of the tribe Andropogoneae. The 12 species recognized by Linnaeus in the first edition of *Species Plantarum* are now distributed among nine genera.

The tribe is a natural assemblage, with a center of distribution in southeastern

TABLE 1. **Number of species (total taxa) recognized in previous taxonomic treatments of Andropogon gyrans, A. virginicus, and A. glomeratus, as delimited in this work.**

	SPECIES (total taxa) RECOGNIZED			
AUTHOR	*gyrans*	*virginicus*	*glomeratus*	Total
Hackel, 1889	1 (3)	1 (5)	1 (5)	3 (13)
Nash, 1903	3	4	3 (5)	10 (12)
Fernald & Griscom, 1935	1 (3)	1 (8)	0	2 (11)
Hitchcock, 1951	3	3 (4)	1	7 (8)
Roberty, 1960	0	1 (7)	0	1 (7)
Radford *et al.*, 1964	2	1	0	3
Long & Lakela, 1971	2	2 (3)	1	5 (6)
Campbell (present paper)	1 (3)	1 (5)	1 (5)	3 (13)

Asia (Hartley, 1950, 1958), and its cohesiveness rests on similarity in many aspects of morphology (Clayton, 1972), cytology (Celarier, 1956, 1957, 1958, 1959), anatomy (Metcalfe, 1960; Chaudra & Saxena, 1964; F. W. Gould, 1967), and biochemistry (Guttierrez *et al.*, 1974). It has been the focus of several major taxonomic studies (Hackel, 1889; Keng, 1939; Roberty, 1960) and has been considered the most advanced tribe of the Gramineae. If one agrees with Stebbins (1974), it is the most advanced taxon of all angiosperms.

Although the tribe is easily circumscribed, the delimitation of its genera has been problematic. Clayton (1972) used a numerical approach based on 41 morphological characters to cluster the genera. He admitted that his findings were tentative and that much remained to be done. For *Andropogon* he accepted Stapf's (1919) classification (1967, and pers. comm.). His concept of the genus is narrow and does not include *Bothriochloa* Kuntze, *Dichanthium* Willimet, or *Schizachyrium* Nees. However, the genus remains large and heterogeneous (F. W. Gould, 1967). The largest of Stapf's four sections, LEPTOPOGON Stapf, contains approximately 55 species (Clayton, pers. comm.), with about 20 in Africa and the balance in the New World. The complex of species centering around *A. virginicus* includes the majority of species of the section that occur in the northern areas of the New World.

Only three species of sect. LEPTOPOGON not included in the virginicus complex have been collected in the United States. *Andropogon ternarius* Michaux (including *A. ternarius* var. *cabanisii* (Hackel) Fernald & Griscom) is common in much of the eastern United States and rare in Mexico. *Andropogon bicornis* L., widespread in South and Central America and the West Indies, has been collected only once in the United States (Florida, Monroe County, *Craighead s.n.*, 1962 (FTG)). *Andropogon gracilis* Sprengel is rather frequent on the Miami oolite of Dade and Monroe counties, Florida. *Andropogon gerardii* Vitman and *A. hallii* Hackel of sect. ANDROPOGON are the only other species of the genus in the United States. South of the United States, 12 other species of sect. LEPTOPOGON occur within the range of the virginicus complex. *Andropogon virgatus* Desv. (probably better treated as *Hypogynium virgatum* (Desv.) Dandy) is morphologically the most distant of these species and will not be considered further. The nine other species outside the virginicus complex in the West Indies are *A. urbanianus* Hitchc., *A. gracilis*, *A. reedii* Hitchc. & Ekman, *A. reinoldii* León, *A. nashianus* Hitchc., *A. lateralis* Nees, *A. leucostachyus* HBK., *A. selloanus* (Hackel) Hackel, and *A. bicornis*. The last four also grow in Central America, and in Mexico along with three Mexican endemics, *A. bourgaei* Hackel, *A. pringlei* Scribner, and *A. spadiceus* Swallen. The four species that occur both east and west of the Gulf of Mexico also extend into South America. The section is well represented there, but only one species, *A. arenarius* Hackel, is very similar to species of the virginicus complex. Finally, *A. leucostachyus* is the only species found in both the New and Old Worlds (possibly introduced into Africa (Stapf, 1919)). Three African species of sect. LEPTOPOGON, *A. eucomus* Nees, *A. huillensis* Rendle, and *A. laxatus* Stapf, resemble the species of the virginicus complex in general aspect but are excluded from the complex on morphological grounds (see below).

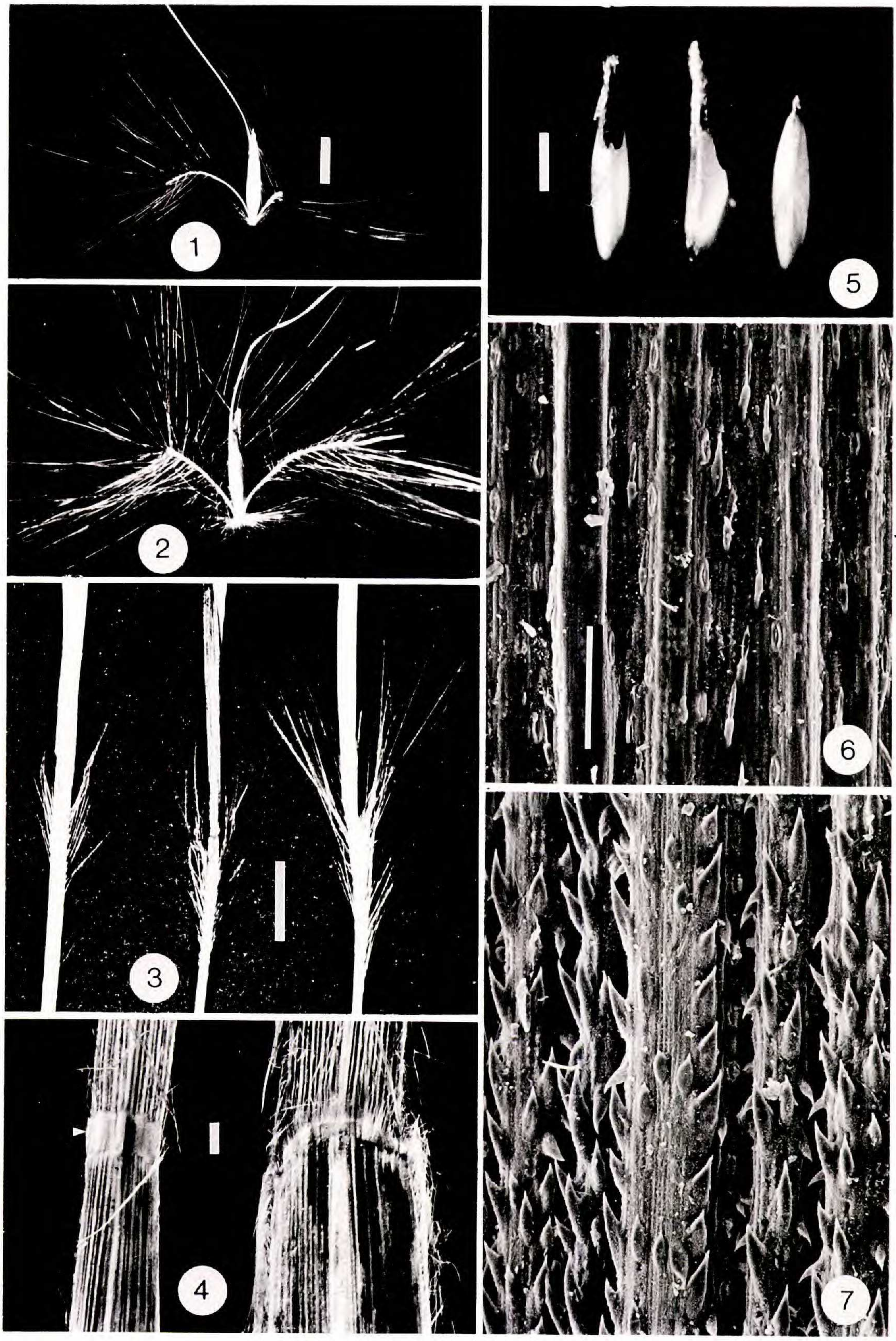
The essential features characterizing all the taxa of the virginicus complex and combining to distinguish them from the other species of sect. LEPTOPOGON are presented in TABLE 2. The reduction in stamen number from three to one, the single most distinctive feature of members of the virginicus complex, is found in many other genera of grasses: *Cinna* L., *Uniola* L. (Booth, 1964), *Stipa* L. (Brown, 1949), *Bothriochloa* (Heslop-Harrison, 1961), *Briza* L. (Murray, 1974), *Imperata* Cyr. (Clifford, 1961), *Deschampsia* Beauv. (Parodi, 1949), *Chikusichloa* Koidz. (Connor, 1979), *Poa* L. (Weatherwax, 1929), and *Vulpia* K. C. Gmelin (Cotton & Stace, 1977). In these genera, as in the virginicus complex, the reduction in stamen number is associated with the capacity for cleistogamy (Campbell, 1982b). The only other species with one stamen in sect. LEPTOPOGON are *Andropogon gracilis* and the two closely related Mexican endemics, *A. pringlei* and *A. spadiceus*. Significantly, all three produce cleistogamous flowers, although cleistogamy in these taxa differs from that in the virginicus complex (Campbell, 1982b). Because *A. gracilis* has one raceme per inflorescence unit, several authors have placed it in *Schizachyrium* (*S. gracile* (Sprengel) Nash). However, it does not have the cupuliform rachis internodes and rounded glumes of the sessile spikelets that Clayton (1964) considered to be important features of *Schizachyrium*. In addition to having solitary racemes, *A. gracilis* differs from the virginicus complex in being tetraploid ($n = 20$; Davidse & Pohl, 1972). *Andropogon pringlei* and *A. spadiceus* differ from the virginicus complex in three morphological characters (TABLE 2).

Of the 16 species listed in TABLE 2, only *Andropogon huillensis* is separated from the virginicus complex in less than two ways. There may be a second difference for this species, depending upon what its chromosome number really is (two different ploidy levels have been reported—see TABLE 2). Six species differ in only two ways. The wide-ranging *A. lateralis* (and the numerous species closely related to it) is quite different from the virginicus complex in having large, functional, pediceled spikelets. For some of the other five species listed in TABLE 2, there are additional differences that are not given in the table. The racemes of *A. selloanus* and *A. eucomus* are more densely pubescent. The lower glumes of *A. nashianus* are ovate in shape and distinctly different from the lanceolate to oblong lower glumes of plants of the virginicus complex. Mor-

TABLE 2. **Comparison of the Andropogon virginicus complex with its closest relatives.**

SPECIES	STAMEN NUMBER	SPIKELET LENGTH (mm)	AWN	AWN BASE TWISTING	PEDICELED SPIKELET	RACHIS INTERNODE	CHROMOSOME NUMBER
A. virginicus complex	1	3–5	Present	Moderate	0 to vestigial	Thin	$n = 10$*
A. arenarius	3	4–6	Usually absent	—	0 to functional	Thin	Unknown
A. bicornis	3	3–4	Absent	—	0 to functional	Thin	$n = 30$ (Pohl & Davidse, 1971)
A. bourgaei	3	ca. 4	Absent	—	0 to functional	Thin	Unknown
A. eucomus	3	2.5–3	Present	Moderate	0 to vestigial	Thin	$n = 10$ (de Wet, 1954)
A. huillensis	3	ca. 4	Present	Moderate	0 to vestigial	Thin	$n = 30$ (de Wet, 1960) $n = 10$ (Dujardin, 1978)
A. lateralis	3	3.5–5	Present	Moderate	0 to functional	Thin	Unknown
A. laxatus	3	4–5	Present	Strong	0 to vestigial	Thin	Unknown
A. leucostachyus	3	2.5–3.5	Absent	—	0 to vestigial	Thin	$n = 10$ (F. W. Gould, 1956)
A. nashianus	3	2.5–3.5	Present	Moderate	0 to vestigial	Thin	Unknown
A. pringlei/spadiceus	1	6–7	Present	Strong	0 to vestigial	Thick	Unknown
A. reedii	3	4–6	Present	Strong	0 to functional	Thin	Unknown
A. reinoldii	3	2.5–3	Present	Moderate	0 to vestigial	Thin	Unknown
A. selloanus	3	ca. 4	Absent	—	0 to vestigial	Thin	$n = 10$ (F. W. Gould, 1956)
A. ternarius	3	5–6.5	Present	Moderate	0 to vestigial	Thick	$n = 20$ (F. W. Gould, 1956)
A. urbanianus	3	4–6	Present	Strong	0 to functional	Thin	$n = 40$ (Davidse & Pohl, 1972)

*See Table 3.



FIGURES 1–7. 1, 2, dispersal units, scale bar = 2 mm: 1, old-field variant of *Andropogon virginicus* var. *virginicus* (*Campbell 3770*); 2, common variant of *A. gyrans* var. *gyrans* (*Campbell 3782*). 3, bases of raceme sheaths showing sparse, moderate, and dense pubescence, bar = 2 mm. 4, ligules (arrow) of *A. glomeratus* var. *glomeratus* (left, *Camp-*

phologically, *A. huillensis, A. reinoldii,* and *A. laxatus* remain as the species closest to the virginicus complex.

The uniformity of the virginicus complex in the features shown in TABLE 2 argues for its naturalness. Other evidence for this supposition comes from the chemical similarity of the taxa. Eighteen of the taxa were surveyed with standard methods of paper chromatography (Mabry *et al.,* 1970): sixteen had nearly identical spot patterns. The two that vary somewhat, *Andropogon arctatus* and the robust variant of *A. glomeratus* var. *pumilus,* differ from the remainder of the virginicus complex in other ways as well. *Andropogon arctatus* has rhizomes, the most primitive flowering mode of the virginicus complex, and a different sort of life history. The robust variant has the widest tolerance for soil salinity and pH of all taxa of the virginicus complex.

GENERAL DESCRIPTION OF THE VIRGINICUS COMPLEX

The yearly growth of plants of the virginicus complex is divided into two phases. In the first part of the season, growth is vegetative in the form of a proaxis of basal leaves with very shortened internodes. In July, August, or September (presumably in response to short day-length, as in other species of the Andropogoneae (Tompsett, 1976)), the proaxis extends rapidly to produce a flowering stem. The stems are terete and 0.2–3.1 m in height.

The leaves may be glabrous or pubescent with unicellular macrohairs; scabrous on the adaxial blade surface and, in some taxa, on the abaxial sheath surface; and glaucous or green. The leaf blades are flattened to occasionally folded, and laxly recurving to infrequently erect. The ligules[1] are membranaceous and 0.2–2.2 mm long, with margins glabrous to long-ciliate.

The inflorescence is a complex branch system. Stapf (1919) described the branching of *Andropogon* as cymose. At each node of plants of the virginicus complex, one to eleven branches may develop on a very short common axis. The largest branch is next to the parent axis, and successively smaller ones arise distally on the common axis. The branches alternate in two ranks that are close to one another on the adaxial side of the common axis. The first structure on the common axis is a two-nerved, hyaline prophyll separating the first branch from the parent axis. Between each of the distal branches there is also a prophyll (FIGURE 10).

The tips of the ultimate branches of the inflorescence bear structures here called inflorescence units (see APPENDIX A and FIGURE 11). The raceme sheath

[1]Certain terms, of a technical nature or specialized in their meaning, are frequently used in this paper. They are defined in APPENDIX A, and some are illustrated in FIGURES 1–11.

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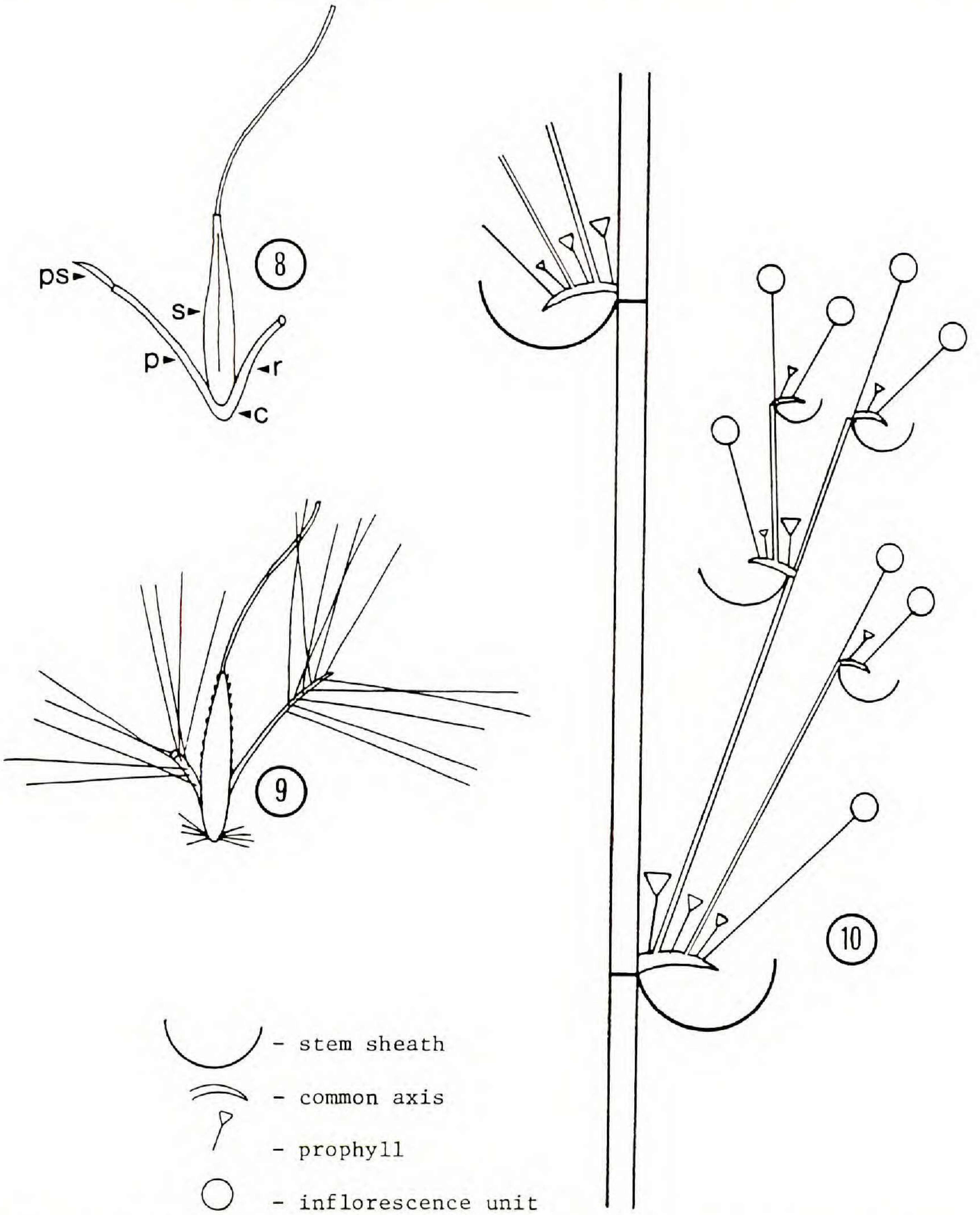
bell 3805) and deceptive variant of *A. virginicus* var. *virginicus* (right, *Campbell 3747*), bar = 1 mm. 5, fruits of common variant of *A. gyrans* var. *gyrans* (*Campbell 3872*) (note marcescent anther at apex of left and center fruits), bar = 1 mm. 6, 7, scanning electron micrographs of stem sheaths, scale bar = 1 μm: 6, deceptive variant of *A. virginicus* var. *virginicus* (*Campbell 3870*) (note bicellular microhairs); 7, *A. glomeratus* var. *glomeratus* (*Campbell 3973*) (note apically directed prickle hairs).



FIGURES 8–10. 8, 9, dispersal units: 8, old-field variant of *Andropogon virginicus* var. *virginicus* (pubescence not included), showing one-keeled upper glume and base of awn; 9, robust variant of *A. glomeratus* var. *pumilus* (many hairs of callus, rachis internode, and pedicel omitted), showing two-keeled lower glume (note prickle hairs extending to below middle of keels of lower glume). 10, diagram of inflorescence node of plant of virginicus complex. c = callus, p = pedicel, ps = pediceled spikelet, r = rachis internode, s = spikelet.

subtends the peduncle, which bears at its apex two or more racemes. The raceme is made up of a straight axis, the rachis, which has four to fourteen nodes. At each node there is a pair of spikelets (a major character for the tribe Andropogoneae). In the virginicus complex, one of the spikelets is sessile and the other is vestigial or entirely absent and represented only by its pedicel. The sessile spikelet has two subcoriaceous glumes. The lower glume has two keels, and the upper glume has one. The glumes enclose two florets, the lower of which is sterile (as in most members of subfam. Panicoideae) and is represented only by a hyaline lemma. The upper floret consists of a long-awned, hyaline lemma, a vestigial (0.4–1.5 mm long) palea, and a flower with two lodicules, one stamen, and a two-styled ovary. The ovary matures into a brownish or purplish caryopsis.

FLOWERING

The 15 taxa observed flower consistently around dawn in the late summer and early fall. Populations in the northeastern United States tend to flower in August and September, and those in the south from September to November. In any region there is great overlap in flowering time between most of the taxa. Exceptions are noted under individual taxa. Vernal flowering occurs in some taxa (e.g., *Andropogon brachystachyus* and especially *A. longiberbis*), apparently in response to burning. In Mexico, Central America, and the West Indies late summer to fall flowering predominates.

Variation in flowering in the virginicus complex is considerable (Campbell, 1982b). *Andropogon arctatus, A. tracyi, A. floridanus, A. brachystachyus,* and some taxa of *A. virginicus* and *A. glomeratus* produce mostly chasmogamous flowers (see character 33 of TABLE 4). The synchrony of peduncle elongation and floral maturation exposes the spikelets above the raceme sheath at anthesis. The lodicules can then open the spikelet. The filament elongates in about an hour, and the anther and styles protrude for potential cross-pollination. If the peduncle does not elongate sufficiently to free the spikelet above the raceme sheath, the lodicules cannot open the spikelet, and cleistogamy results.

When the peduncle does not elongate appreciably, the combined action of many lodicules forces the racemes out between the margins of the raceme sheath. The lodicules then open the spikelets. If, however, the flowers mature before the inflorescence unit emerges from the stem sheath in which it developed, the lodicules cannot open the spikelets. Cleistogamy is far more common in short-peduncled than in long-peduncled racemes (see character 33 of TABLE 4).

CHROMOSOME NUMBERS

Counts of a haploid chromosome number of 10 have been made for all species and for 16 of the 21 taxa (TABLE 3). Because of the possibility of misidentification of these morphologically close grasses, published reports are less reliable than those for which a voucher has been examined. The two polyploid counts reported for *Andropogon virginicus* are strongly questioned because of the uniform diploidy of the complex. The count of $2n = 40$ may have been based on a mitotic division in the anther similar to the one shown in FIGURE 16. The chromosomes appear to be meiotic, and the nucleolus marks

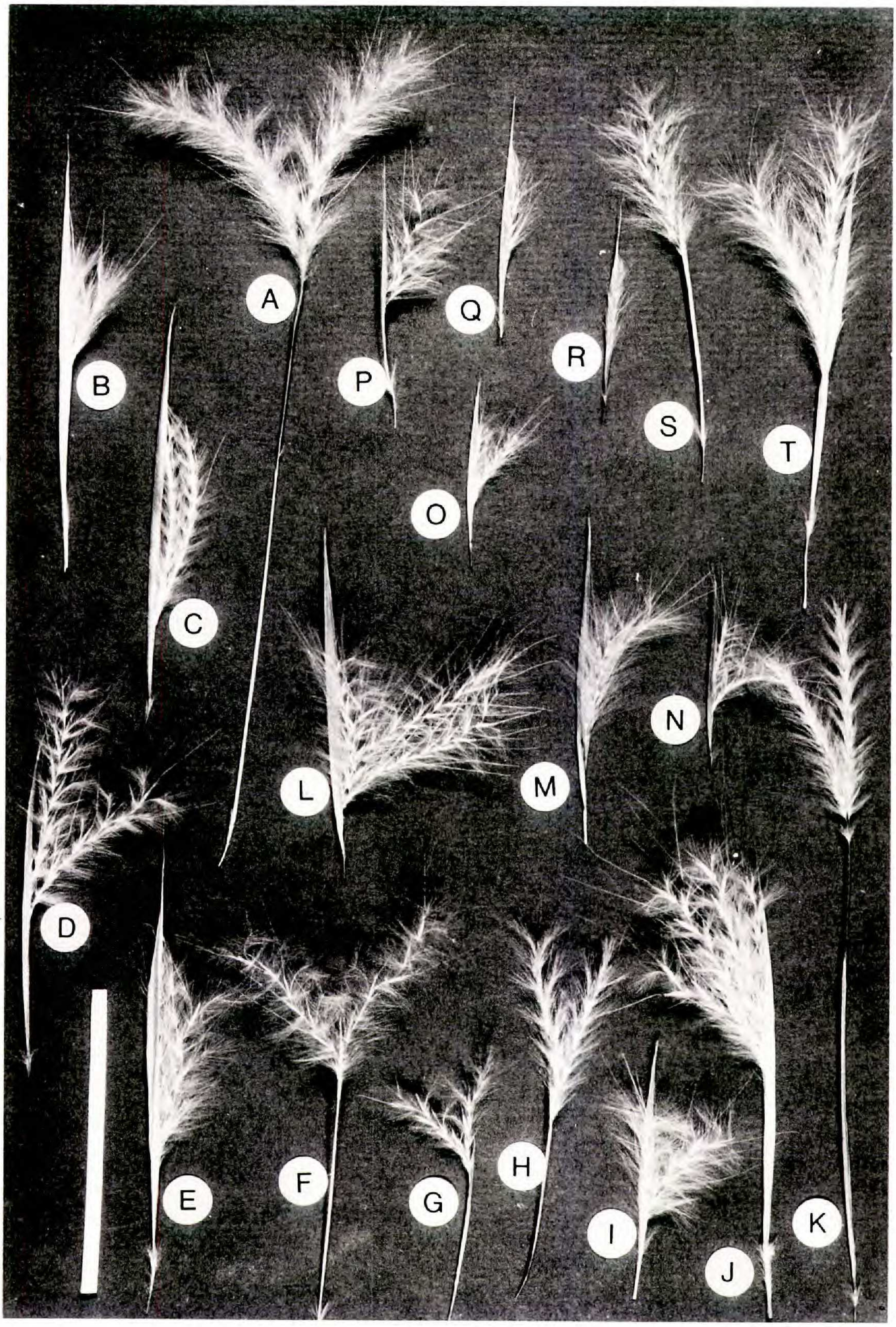


FIGURE 11. Inflorescence units: A, B, common variant of *Andropogon gyrans* var. *gyrans* (*Campbell 3872*); C, D, *Andropogon gyrans* var. *stenophyllus* (*Campbell 3822*); E, F, tenuous variant of *A. gyrans* var. *gyrans* (*Campbell 3873*); G, *A. brachystachyus* (*Campbell 3884*); H, *A. floridanus* (*Campbell 3754*); I, *A. longiberbis* (*Campbell 3729*); J, *A. liebmannii* var. *pungensis* (*Campbell 3948*); K, *A. arctatus* (*Campbell 3944*); L, M,

the stage as prophase, but another cell from the same anther, a pollen mother cell in prophase I, showed ten bivalents.

For the 16 counts reported in this work, young spikelets were fixed in Farmer's solution (3 parts 100% ethyl alcohol, 1 part glacial acetic acid), transferred to 70% ethyl alcohol after 24 hours, and stored at about 4°C. Fixation early in the morning yielded far more meiotic figures than that done later in the day. The ten new counts reported here are shown in FIGURES 12–21. In all taxa studied the basipetal sequence of floral maturation facilitated finding prophase I to anaphase I. In racemes of wholly chasmogamous flowers, the developmental gradient is steeper than in those with cleistogamous flowers. In the former group, one raceme may contain nearly mature pollen in the apical spikelets and pollen mother cells in the basal spikelets. In contrast, meiosis may occur concurrently in all flowers of a raceme in the frequently or predominantly cleistogamous taxa.

GEOGRAPHIC DISTRIBUTION

Eighteen of the taxa grow on the Coastal Plain of the southeastern United States (see MAP 1). The distribution of 12 is entirely limited to the region extending from southernmost New Jersey to eastern Texas. *Andropogon arctatus, A. floridanus, A. longiberbis,* and *A. brachystachyus* grow principally in Florida and infrequently in nearby states or the Bahamas. Only one taxon of eastern United States broomsedges, *A. liebmannii* var. *pungensis,* does not occur extensively in Florida.

The common variant of *Andropogon gyrans* var. *gyrans,* the old-field variant of *A. virginicus* var. *virginicus,* the robust variant of *A. glomeratus* var. *pumilus,* and the two varieties of *A. liebmannii* show a pattern of eastern United States–Mexican distributions common to many other vascular plants (Graham, 1973). Because of the uncertainties about the phytogeographic relationships of these two regions and the paucity of andropogonoid fossils, assertions concerning the direction of migration are conjectural. However, one line of reasoning suggests migration from the center of distribution to Mexico. This rests on the hypothesis (developed more fully in the discussion under *A. brachystachyus*) that *A. virginicus* is derived from *A. brachystachyus* ancestry. The range of the latter taxon and most of the variants of *A. virginicus* is restricted to the southeastern United States. Only the old-field variant of var. *virginicus* grows in Mexico, possibly after migration there.

Closely related taxa in *Andropogon virginicus* and *A. glomeratus* have the

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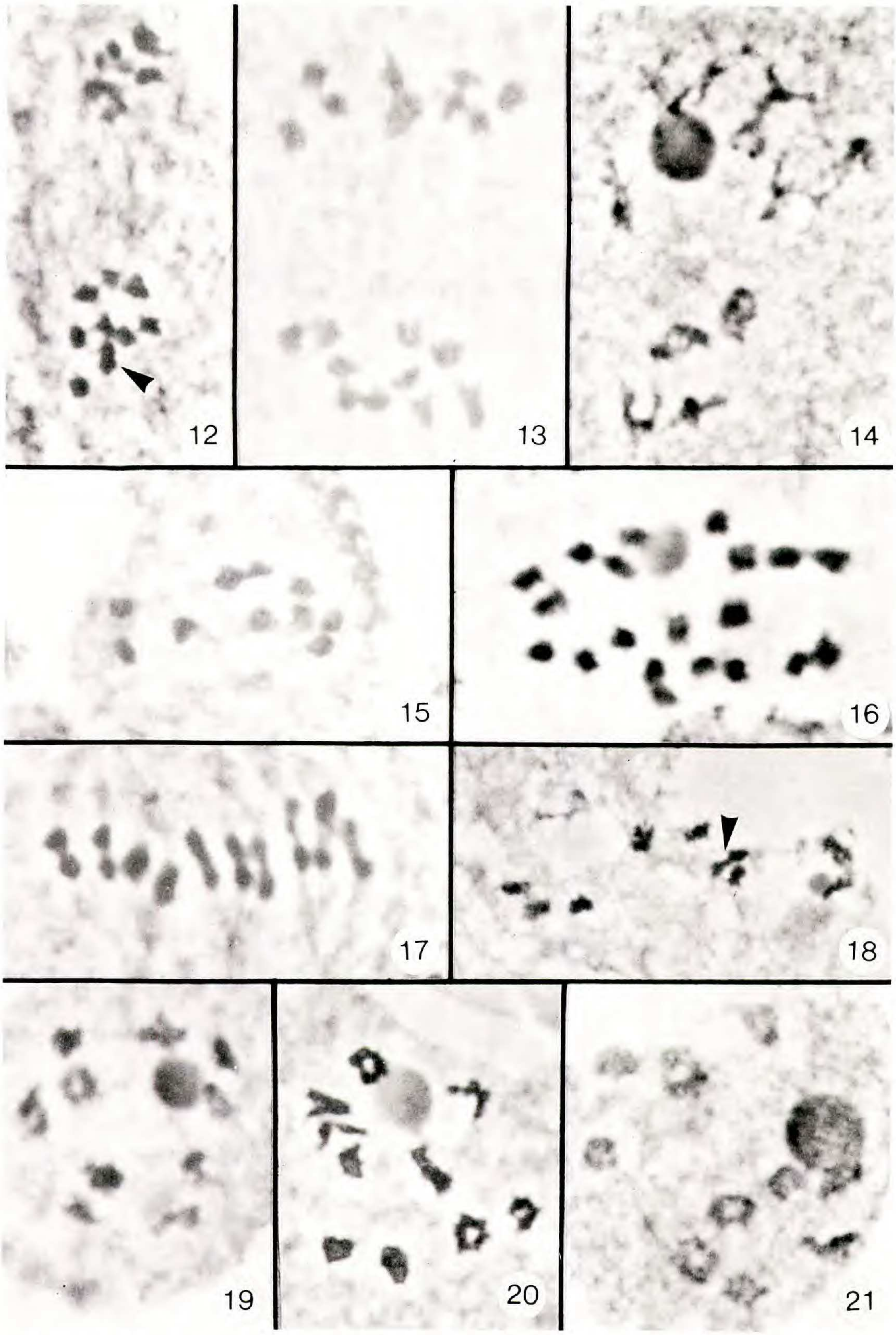
old-field variant of *A. virginicus* var. *virginicus* (*Campbell 3849*); N, deceptive variant of *A. virginicus* var. *virginicus* (*Campbell 4081*); O, drylands variant of *A. virginicus* var. *glaucus* (*Campbell 3898*); P, robust variant of *A. glomeratus* var. *pumilus* (*Campbell 3850*); Q, *A. glomeratus* var. *hirsutior* (*Campbell 3804*); R, *A. glomeratus* var. *glaucopsis* (*Campbell 3806*); S, *A. glomeratus* var. *glomeratus* (*Campbell 3915*); T, *A. tracyi* (*Campbell 4100*). Bar = 5 cm.

TABLE 3. **Chromosome numbers in the Andropogon virginicus complex.**

TAXON	COUNT	LOCALITY	VOUCHER SPECIMEN OR REFERENCE
A. arctatus	$n = 10$	Florida, Liberty Co.	*Campbell 4060* (GH)
A. brachystachyus	$n = 10$	Florida, Putnam Co.	*Campbell 4264* (GH)
A. floridanus	$2n = 20$	No locality given	Carnahan & Hill, 1961
	$n = 10$	Florida, Marion Co.	*Campbell 4194* (GH)
A. glomeratus	$n = 10$	No locality given	Church, 1936
var. **glaucopsis**	$2n = 20$	Florida, Duval and St. Johns cos.	Church, 1940
var. **glomeratus**	$n = 10$	Massachusetts, Plymouth Co.	*Campbell 3973* (GH)
	$2n = 20$	Rhode Island, Washington Co.	Church, 1940
var. **hirsutior**	$n = 10$	Georgia, Berrien Co.	*Celarier* (MO)
		Alabama, Baldwin Co.	*Campbell 3804* (GH)
var. **pumilus**			
robust variant	$n = 10$	Texas, Fort Bend Co.	F. W. Gould, 1956
		Georgia, Berrien Co.	*Celarier A-2600-1* (MO)
		Alabama, Montgomery Co.	*Campbell 3958* (GH)
		No locality given	*Gage s.n.* (MO)
		Mexico, Veracruz	*Campbell 3648* (GH)
		Dominican Republic, Espaillat	Davidse & Pohl, 1972
	$2n = 20$	Texas, Robertson Co.	Church, 1940
		Texas, no county given	Brown, 1950
		Mexico, Chiapas	F. W. Gould & Soderstrom, 1970
A. gyrans			
var. **gyrans**			
common variant	$n = 10$	Louisiana, Rapides Parish	*Gould RF 506* (TAES)
		Georgia, Tift Co.	*Celarier A-2608-1* (MO)
		Florida, Jackson Co.	*Campbell 3815* (GH)

	$2n = 20$	Georgia, McIntosh Co.	Church, 1940
		Mexico, Chiapas	Tateoka, 1962
tenuous variant	$n = 10$	Florida, Highlands Co.	*Campbell 3746* (GH)
var. **stenophyllus**	$n = 10$	Florida, Liberty Co.	*Campbell 4259* (GH)
A. longiberbis	$n = 10$	Florida, Dade Co.	*Campbell 3734* (GH)
A. liebmannii			
var. **pungensis**	$n = 10$	Alabama, Washington Co.	*Campbell 3695* (GH)
A. tracyi	$n = 10$	Florida, Putnam Co.	*Campbell 4100* (GH)
A. virginicus			
var. **glaucus**			
wetlands variant	$n = 10$	Florida, Jackson Co.	*Campbell 3818* (GH)
var. **virginicus**	$n = 10$	Massachusetts, Barnstable Co.	Church, 1936
		Texas, Robertson and San Augustine cos.	F. W. Gould, 1956
	$2n = 20$	Virginia, Princess Anne Co.	Church, 1940
	$2n = 40$*	Tennessee, no county given	*Alava 3246, 3252* (MO)
	$n = 40$*	No locality given	Mohlenbrock, 1973
deceptive variant	$n = 10$	Florida, Jackson Co.	*Campbell 3778* (GH)
old-field variant	$n = 10$	Rhode Island, Washington Co.	*Celarier A-2620-1* (MO)
		Georgia, Berrien Co.	*Celarier A-2607-1* (MO)
		Florida, Jackson Co.	*Campbell 3782* (GH)
		Florida, Putnam Co.	*Campbell 4265* (GH)

*Probably misinterpretations.



FIGURES 12–21. Chromosomes (see TABLE 3 for voucher data; unless otherwise noted, all meiotic figures): 12, *Andropogon floridanus*, anaphase, × 720; 13, deceptive variant of *A. virginicus* var. *virginicus*, anaphase, × 720; 14, *A. tracyi*, diakinesis, × 720; 15, *A. liebmannii* var. *pungensis*, diakinesis, × 865; 16, *A. gyrans* var. *stenophyllus*, mitotic prophase in an anther, × 965; 17, *A. brachystachyus*, metaphase, × 825; 18, *A. longi-*

most similar ranges. The wetlands, drylands, deceptive, and smooth variants of the former and *Andropogon glomeratus* vars. *glaucopsis* and *hirsutior* are found on the Coastal Plain of the southeastern United States, especially from southern Virginia and Mississippi (MAPS 13–16, 18, 19).

ECOLOGY

The requirements of high levels of sunlight and little competition usually confine populations of the virginicus complex to areas undergoing early succession or to persistently disturbed sites; they characteristically grow along roadsides or under powerlines, or they invade abandoned agricultural land or clear-cut timberlands (FIGURES 22–27). The old-field variant of *Andropogon virginicus* var. *virginicus* is so successful as a colonizer (Keever, 1950; Golley, 1956; Bazzaz, 1975) that the three- to five-year period after an environmental opening has occurred is called the broomsedge stage.

The success of members of the virginicus complex as weeds is certainly due in part to their dispersibility, both locally and to newly available sites. The long, spreading hairs of the dispersal unit provide aerodynamic drag for wind dispersal; the terminal velocity of the dispersal units is roughly equivalent to that of the common dandelion (Campbell, 1983). Because they are considerably taller than dandelions, the individual broomsedge plants have a greater potential dispersal range. The probability of their long-distance dispersal increases through their capacity for autogamy. The increase in homozygosity that accompanies inbreeding apparently promotes close adaptation to a particular environment (Allard, 1975). The most successful colonizers of the virginicus complex—the common variant of *Andropogon gyrans* var. *gyrans,* the old-field and deceptive variants of *A. virginicus* var. *virginicus,* and *A. glomeratus* vars. *hirsutior* and *glaucopsis*—bear mostly cleistogamous flowers. The one notable exception to this generality is the robust variant of *A. glomeratus* var. *pumilus.*

These andropogons will flourish in partial shade if competition is suppressed through fire. In two pine plantations in the southeastern United States, there are extensive populations of the virginicus complex where annual burns prevent hardwood growth. Over large areas in both localities, the fall reproductive growth of the broomsedges dominates the undergrowth (FIGURE 26). At the plantation in Thomas County, Georgia, there are large populations of eight taxa of the complex, and at the Bladen County, North Carolina, site six taxa grow together. Clayton (1969) pointed to a possible adaptation for fire ecology of *Hyparrhenia* Andersson of the Andropogoneae in the demonstrated ability of their dispersal units to bury themselves. The hygroscopic awn and the callus

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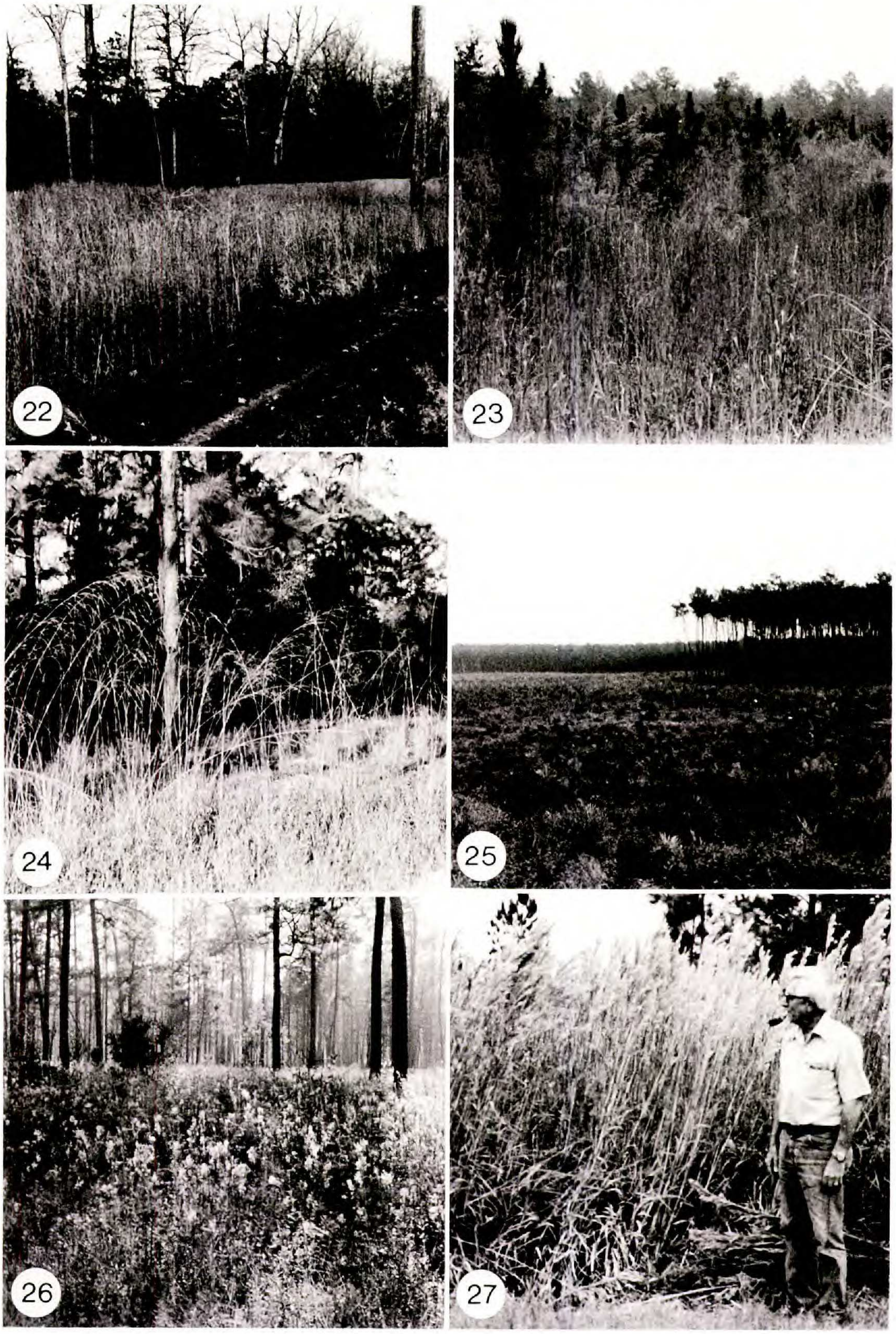
berbis, diakinesis, × 715; 19, wetlands variant of *A. virginicus* var. *glaucus,* diakinesis, × 790; 20, tenuous variant of *A. gyrans* var. *gyrans,* diakinesis, × 940; 21, *A. arctatus,* diakinesis, × 715. (Arrows in 12 and 18 indicate two bivalents not resolvable in this focal plane.)



FIGURES 22–27. 22, 23, old-field variant of *Andropogon virginicus* var. *virginicus*: 22, under powerline, Kent Co., Maryland; 23, in four-year-old *Pinus elliottii* timberland, Decatur Co., Georgia. 24, *A. brachystachyus*, in clearing in flatwoods, Highlands Co., Florida. 25, clear-cut *P. clausa* timberlands colonized by *A. floridanus*. 26, several taxa

hairs work the spikelet into the soil, where it is more protected from fire. The broomsedge dispersal unit may function in the same way, although the awn is often barely twisted (and therefore weakly hygroscopic).

Most of the taxa of the virginicus complex have rather narrow tolerance for soil moisture. For example, in the panhandle of Florida, one characteristically finds the wetlands variant of *Andropogon virginicus* var. *glaucus* at the bottom of roadside ditches. *Andropogon gyrans* var. *stenophyllus* often borders the same ditches, and above the ditches one is likely to see the deceptive variant of *A. virginicus* var. *virginicus,* the common variant of *A. gyrans* var. *gyrans,* and the drylands variant of *A. virginicus* var. *glaucus.* The old-field variant of var. *virginicus,* tolerant of a wide variety of soil moisture conditions, may occur anywhere on the slope.

While human activity has been decidedly beneficial to these broomsedges, the plants are commercially undesirable since they supplant other vegetation of greater economic value as fodder. Cattle generally eschew most of these andropogons. The only direct economic value of the plants is in their leaves and stems, which have long been used for dyeing fabric and for brooms.

EVOLUTION AND SPECIATION

A dominant trend in the evolution of the virginicus complex has been the shift from chasmogamy to cleistogamy. Stebbins (1957) presented convincing evidence for the primitive nature of outcrossing and the derived condition of inbreeding. The derivation of cleistogamy in the virginicus complex involved shortening the peduncle and developmental shifts in the maturation of the flowers (Campbell, 1982b). Smaller spikelets and anthers and increased weediness are often associated with a shift toward cleistogamy. The reduction in anther length and pollen-producing capacity may result from relaxed selection for the copious pollen needed for wind pollination.

Evidence suggests that the change from chasmogamy to cleistogamy has repeatedly occurred in the virginicus complex (Campbell, 1982b). Both the tenuous variant of *Andropogon gyrans* var. *gyrans* and var. *stenophyllus* of the same species consist of two kinds of plants, one with some long peduncles and chasmogamous flowers and one with all short peduncles and mostly cleistogamous flowers. The plants are otherwise similar, but the cleistogamous form of both taxa is more widespread and common.

Another derivation of cleistogamy involves the precocious sexual maturation of ancestors of *Andropogon brachystachyus* to produce the deceptive variant of *A. virginicus* var. *virginicus* and, by other character changes, the rest of *A. virginicus.* Finally, *A. glomeratus* var. *glomeratus* appears to be the ancestral stock for both vars. *hirsutior* and *glaucopsis.*

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of *A. gyrans, A. virginicus,* and *A. glomeratus* in annually burned *P. palustris* plantation, Thomas Co., Georgia. 27, robust variant of *A. glomeratus* var. *pumilus* in roadside ditch, Putnam Co., Florida.

Cleistogamy presumably brings to the virginicus complex both greater colonizing ability (see ecology section) and a barrier to gene flow between the taxa (Campbell, 1982b). This barrier contributes to the reproductive isolation of the taxa that grow together. Mixed populations of broomsedges are so common now that one might assume that they have always grown together and that speciation was sympatric. Cleistogamy might have provided the interruption in gene flow essential to divergence. However, the phenomenon of mixed populations may have developed largely in the presence of man's tremendous disturbance of the habitat. The taxa that are so common today may once have been restricted to infrequent openings caused by fire and other natural disturbance. Their divergence from one another may have taken place in isolation in pre-Columbian times.

Many of the taxa that frequently grow near one another in mixed populations are very closely related. For example, two varieties of *Andropogon glomeratus*, vars. *hirsutior* and *glaucopsis*, form mixed populations in 67 percent of the 28 populations I have studied (Campbell, 1980). I have not detected plants of intermediate morphology that would suggest gene flow between these or most of the other closely related taxa.

HYBRIDIZATION

Hybridization between taxa of the virginicus complex is rare. There are ample opportunities for gene flow between taxa because they frequently grow together and flower at the same time of day and (mostly) at the same time of year. I have observed two taxa growing within one to three meters of one another over four hundred times. In only five of these opportunities for hybridization were there plants whose intermediate morphology suggested that they were hybrids. In the rare instances when hybridization does take place, there are few mature hybrid individuals. I have found only twelve putative hybrid individuals in the five localities where hybridization is suspected. The parents outnumber these hybrids by between five and one hundred or more to one.

Four of the suspected hybridizations involve the old-field variant of *Andropogon virginicus* var. *virginicus*. *Andropogon longiberbis* and the robust variant of *A. glomeratus* var. *pumilus* are the other parents in two cases each. In the fifth instance the robust variant and *A. longiberbis* produced six putative F_1 plants.

In all these instances the putative hybrids are morphologically intermediate between the parents. The three putative F_1 hybrids of the old-field variant and *Andropogon longiberbis* fall between the parents in the orientation of sheath pubescence, the number of racemes per inflorescence unit, and the lengths of the racemes, spikelets, and callus hairs. The three putative hybrids of the old-field and robust variants are intermediate in leaf-blade and raceme-sheath width and in maximum number of inflorescence branches. In leaf-blade length and number of inflorescence units per stem, however, the hybrids from both populations exceed the mean of these characters for both parents. For the robust variant and *A. longiberbis* there are ten characters distinguishing the parents for which the putative hybrids are more or less intermediate: stem height, leaf-

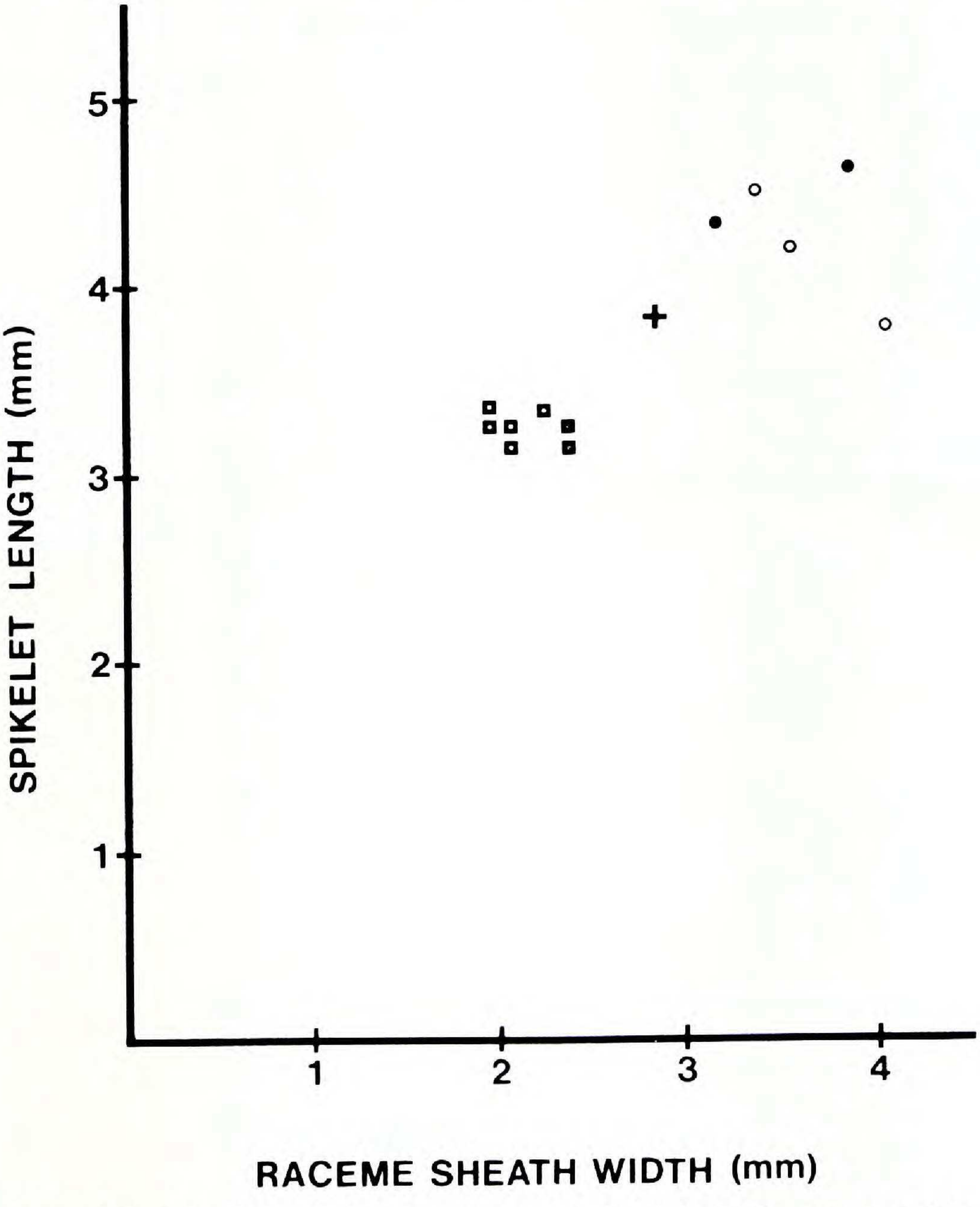

FIGURE 28. Graph of spikelet length vs. raceme-sheath length for seven populations each of robust variant of *Andropogon glomeratus* var. *pumilus* (squares) and *A. longiberbis* (circles; darkened circles indicate two populations with identical values), and for six putative hybrid individuals represented by *Campbell 4266*, Lake County, Florida (cross). Each symbol shows mean of four or five parent plants or six hybrids. Value for each individual is mean of ten measurements of spikelets and raceme sheaths.

pubescence orientation, leaf-blade length and width, number of inflorescence units per stem, raceme-sheath width, peduncle length, spikelet length, callus-hair length, and spikelet-keel scabrousness. Two of the best characters for distinguishing the two parent taxa are raceme-sheath width and spikelet length (FIGURE 28). Variation in these characters for the two parents and the six putative hybrids has been analyzed using discriminant functions (Campbell, 1982a). The six putative hybrids are relatively much less fertile than either parent.

I have observed only two barriers to gene flow in the virginicus complex: cleistogamy and, less importantly, nonsynchronous flowering. Interspecific pollen-style incompatibility, in need of further study, may also contribute to reproductive isolation.

MORPHOLOGY IN RELATION TO TAXONOMY

TABLE 4, which contains information concerning the taxonomically useful variation in the virginicus complex, replaces separate descriptions for the taxa. This format facilitates comparisons between the character states of different taxa and may be used as a multiple-entry key. An explanation of the measurements and abbreviations used is presented in the "Character States" section on pages 194–199.

The first 11 of the 33 characters listed in TABLE 4 pertain to vegetative parts of the plants. Stem height and leaf-blade dimensions vary together and divide the virginicus complex into three rough groups: *Andropogon glomeratus* and *A. floridanus* have the largest dimensions for these characters; *A. gyrans, A. tracyi,* and *A. liebmannii* var. *liebmannii* have the smallest; the rest are mostly intermediate. Because of the overlap between many of the taxa for these characters, they are secondary in importance. Much of the overlap is apparently due to phenotypic response to varying levels of soil moisture and nutrients.

The glaucousness of the leaves and stem internodes of certain taxa is due to a wax that can be rubbed off. It is most conspicuous on young, fresh material. Glaucousness of the leaf is a more reliable character than that of the stem, and it distinguishes both *Andropogon glomeratus* var. *glaucopsis* and *A. virginicus* var. *glaucus* from all other taxa. Infrequently, the leaves of the smooth variant of *A. virginicus* var. *virginicus* are somewhat glaucous.

Variability in the amount and distribution of two types of trichomes is taxonomically useful. The first type is the macroscopic, unicellular hair found on the leaves, below the raceme sheaths, and in the racemes. In this work "pubescence" refers to these hairs. Glabrous leaves lack such hairs. Generally the best place to find pubescence on leaves that are sparsely hairy is near the collar. Glaucous leaves are generally glabrous. Leaf pubescence may disappear as the foliage ages and may also become more appressed. It is therefore best to examine young leaves when trying to determine whether pubescence is spreading or appressed.

The second type of trichome is the microscopic prickle hair; these hairs are usually directed apically on the leaves and keels of the lower glume of the spikelets. When sufficiently abundant, as in plants of *Andropogon glomeratus* (FIGURE 7) and *A. floridanus,* they make the stem sheath scabrous. Pressing the stem sheath firmly with the tip of the finger and moving the finger down the sheath will indicate the absence or the sandpapery effect of the presence of these prickles. They are generally best developed near the collar.

The length of the ligule and its marginal ciliations (FIGURE 4) and the color of the ligule are useful characters; they separate most of *Andropogon glomeratus* from the remainder of the virginicus complex. Previous authors have noted the characteristically long ligules of *A. gyrans* var. *stenophyllus.*

Inflorescence shape is the most conspicuous character of the broomsedges. Since there is considerable variation in this character, authors of earlier works have focused on it and have been confused by the taxa with similar shapes. For example, the range of inflorescence shapes of the robust variant of *Andropogon glomeratus* var. *pumilus* (FIGURE 51) includes those of the rest of *A. glomeratus, A. floridanus* (FIGURE 40), and parts of *A. virginicus* (FIGURES 42, 45) and *A. longiberbis* (FIGURE 41). The similarity of inflorescence shape in *A. glomeratus* and *A. virginicus* is one important factor in the union of the two species by recent American authors (see TABLE 1).

Andropogon brachystachyus and sometimes the drylands variant of *A. virginicus* var. *glaucus* produce long inflorescence branches that spread away from the main stem in smooth arches (FIGURES 24, 43, 44), allowing ready distinction of these plants in the field. Herbarium specimens of these two taxa tend to have rather open inflorescences.

Characters 14 and 15 are attempts to quantify the denseness of the inflorescence. Order of branching refers to the number of rebranchings. For example, FIGURE 10 depicts third-order branching (i.e., three branches at the stem node). These two characters and the number of inflorescence units per stem divide the virginicus complex into three groups that correspond roughly with the groups based on vegetative size. Like stem height and leaf-blade dimensions, they often reflect the suitability of a particular individual's growing conditions. Most of the remaining characters vary independently of stem and leaf dimensions, inflorescence density, and environmental conditions.

Categories of pubescence density below the raceme sheath are shown in FIGURE 3. Seven of the 20 taxa express more than half of the states for this character. There is no overlap in character states in only 25 of the 190 different pairwise combinations of taxa.

The location of the raceme sheath is unique in the common variant of *Andropogon gyrans* var. *gyrans.* Toward the apex of the stem, the internodes are shortened and the stem sheaths become inflated and strongly overlapping. The inflorescence units remain mostly concealed within these inflated stem sheaths. Even though some of the peduncles may elongate and expose the racemes, their subtending raceme sheaths are rarely visible until senescence (FIGURES 29, 30).

Raceme-sheath dimensions, particularly the width, are very useful in distinguishing many of the taxa because of nonoverlapping ranges of mean low and high measurement values.

Peduncle length, spikelet length and width, anther length, and mean percent chasmogamy reflect flowering mode. Mostly chasmogamous plants have long peduncles, large spikelets, and large anthers that are not marcescent at the apex of the fruit within the spikelet (Campbell, 1982b). Plants with predominantly cleistogamous flowers have short peduncles and smaller spikelets and stamens, and the anthers are usually marcescent within the spikelets (see below).

Raceme number distinguishes *Andropogon liebmannii* and is often helpful

TABLE 4. **Character states.**

Character number:		1	2	3	4
		Stem		Leaf	
Taxon	Sample size	height (m.)	glaucousness	glaucousness	pubescence amount
ARCT	17 (8)	(0.9) 1.3 (1.7)	0 (1)	0	0 to D
GYRA	68 (28)	(0.3) 0.8 (1.4)	(0) 1 (2)	0	0 to D
GYRA	37 (17)	(0.5) 0.8 (1.4)	(0) 1 (2)	0	0 to D
comm	23 (10)	(0.5) 0.8 (1.4)	(0) 1	0	0 to D
tenu	14 (7)	(0.5) 0.8 (1.0)	(0) 1 (2)	0	0 to S
STEN	31 (11)	(0.3) 0.7 (1.0)	0,1 (2)	0	0 (S)
TRAC	13 (7)	(0.5) 0.8 (1.2)	0,1	0	0 to S
LIEB	12 (11)	(0.2) 0.9 (1.7)	0	0	S to D
LIEB	6 (5)	(0.2) 0.6 (0.9)	0	0	S to D
PUNG	6 (6)	(0.8) 1.2 (1.7)	0	0	M to D
FLOR	18 (8)	(0.7) 1.4 (2.1)	0 (1)	0	0 (S)
LONG	38 (13)	(0.5) 0.9 (1.5)	0,1	0	S to D
VIRG	147 (75)	(0.4) 1.2 (2.1)	0,1,2	0,1	0 to D
VIRG	98 (43)	(0.4) 1.2 (2.1)	0,1,2	0,1	0 to D
oldf	61 (26)	(0.4) 1.2 (2.1)	0,1	0	S to D
dece	19 (10)	(0.7) 1.2 (1.7)	0	0	S to M
smoo	18 (7)	(0.9) 1.4 (1.8)	2	0,1	0
GLAU	49 (32)	(0.6) 1.2 (1.8)	2	1	0
dryl	20 (15)	(0.7) 1.2 (1.8)	2	1	0
wetl	29 (17)	(0.6) 1.2 (1.7)	2	1	0
BRAC	11 (7)	(1.1) 1.9 (3.1)	0	0	S
GLOM	111 (63)	(0.6) 1.3 (2.5)	0 (2)	0,1	0 to D
GLOM	25 (10)	(0.6) 1.0 (1.6)	0	0	(0) S to D
HIRS	25 (16)	(1.0) 1.4 (2.0)	0	0	(0) S to D
GLAP	22 (13)	(1.2) 1.6 (2.2)	2	1	0 (S)
PUMI	39 (24)	(0.2) 1.4 (2.5)	0	0	0 to D
robu	24 (14)	(0.2) 1.4 (2.5)	0	0	(0) S to D
sout	15 (10)	(0.8) 1.2 (1.5)	0	0	0 to S

in separating the old-field and smooth variants of *A. virginicus* var. *virginicus* from the rest of the virginicus complex. The racemes of the drylands variant of *A. virginicus* var. *glaucus*, the deceptive variant of *A. virginicus* var. *virginicus*, *A. brachystachyus*, and *A. glomeratus* var. *glaucopsis* are shorter than those of other taxa.

The remaining characters pertain to structures of the dispersal unit. The rachis internodes of *Andropogon floridanus* are uniformly pubescent for their full length and do not become glabrous toward the base, as in other taxa. The

TABLE 4. **Character states** (*continued*).

	5	6	7	8
			Leaf Blade	
Taxon	Leaf pubescence orientation	Sheath scab-rousness	length (cm.)	width (mm.)
ARCT	A,S	0	(15) 21 (35)	(3.0) 4.5 (8.0)
GYRA	S (A)	0	(6) 18 (48)	(0.8) 2.2 (5.0)
GYRA	S (A)	0	(8) 20 (48)	(1.4) 2.3 (5.0)
comm	S (A)	0	(8) 20 (48)	(1.4) 2.6 (5.0)
tenu	S	0	(11) 21 (30)	(1.5) 2.0 (3.0)
STEN	S	0	(6) 11 (28)	(0.8) 1.8 (3.0)
TRAC	S	0	(10) 16 (22)	(1.2) 1.9 (2.6)
LIEB	S	0 (1)	(3) 16 (35)	(2.5) 4.4 (7.5)
LIEB	S	0 (1)	(3) 8 (15)	(2.5) 4.2 (6.5)
PUNG	S	0	(15) 24 (35)	(2.5) 4.6 (7.5)
FLOR	S	0,1	(32) 42 (61)	(2.9) 3.8 (5.0)
LONG	A (S)	0	(11) 26 (50)	(2.0) 3.2 (5.5)
VIRG	S	0 (1)	(11) 25 (52)	(1.7) 3.6 (6.5)
VIRG	S	0 (1)	(11) 28 (52)	(1.7) 3.3 (5.5)
oldf	S	0 (1)	(11) 30 (52)	(1.7) 3.0 (5.0)
dece	S	0	(15) 24 (35)	(2.5) 3.6 (5.5)
smoo	-	0	(22) 27 (38)	(2.3) 3.5 (5.0)
GLAU	-	0	(12) 19 (38)	(2.0) 4.3 (6.5)
dryl	-	0	(12) 17 (27)	(2.0) 3.5 (5.0)
wetl	-	0	(13) 20 (38)	(2.6) 4.9 (6.5)
BRAC	S	0	(21) 33 (54)	(2.3) 3.7 (6.0)
GLOM	S (A)	1 (0)	(13) 41 (109)	(2.9) 4.8 (9.5)
GLOM	S	1	(16) 37 (55)	(2.8) 4.3 (7.5)
HIRS	S	1 (0)	(24) 41 (60)	(2.0) 4.2 (6.0)
GLAP	S	0 (1)	(33) 40 (75)	(3.0) 5.0 (7.0)
PUMI	S (A)	0,1	(13) 44 (109)	(3.0) 5.4 (9.5)
robu	S (A)	0,1	(13) 46 (109)	(3.0) 6.0 (9.5)
sout	S	1	(30) 41 (66)	(3.5) 4.4 (6.0)

length of the callus hairs is positively correlated with the general density of hairs on all parts of the dispersal unit. *Andropogon gyrans* and *A. longiberbis*, with callus hairs often to 5 mm long, have more densely pubescent rachis internodes and pedicels than all other taxa except *A. floridanus*. The keels of the lower glumes of the spikelets bear prickles that often extend below the middle of the glume in *A. arctatus* and *A. glomeratus* var. *pumilus*. The awn of the fertile lemma is more or less twisted where it joins the lemma and is relatively short in *A. arctatus*, *A. floridanus*, and *A. brachystachyus*. Variation

TABLE 4. **Character states** (*continued*).

	9	10	11
	Ligule		
Taxon	length (mm.)	ciliation length (mm.)	color
ARCT	(0.3) 0.6 (0.9)	0-0.5	Brown
GYRA	(0.3) 0.9 (1.5)	0-0.7	Light brown (brown)
GYRA	(0.3) 0.6 (1.1)	0-0.3	Light brown to brown
comm	(0.3) 0.6 (1.1)	0-0.7	Light brown
tenu	(0.4) 0.6 (0.8)	0-0.3	Light brown to brown
STEN	(0.8) 1.1 (1.5)	0-0.1	Light brown
TRAC	(0.2) 0.4 (0.5)	0.2-0.8	Brown
LIEB	(0.5) 0.8 (1.2)	0-0.4	Whitish to light brown
LIEB	(0.5) 0.7 (1.9)	0-0.2	Whitish to light brown
PUNG	(0.7) 0.9 (1.2)	0-0.4	Whitish to light brown
FLOR	(0.4) 0.7 (1.2)	0.2-1.3	Brown
LONG	(0.2) 0.4 (0.6)	0.3-0.6	Light brown to brown
VIRG	(0.2) 0.5 (1.0)	0.2-1.3	Brown (light brown)
VIRG	(0.2) 0.5 (1.0)	0.2-1.3	Brown (light brown)
oldf	(0.2) 0.5 (0.8)	0.2-1.3	Brown
dece	(0.3) 0.5 (0.7)	0.5-1.1	Brown
smoo	(0.4) 0.6 (1.0)	0.3-0.9	Brown (light brown)
GLAU	(0.2) 0.4 (0.5)	0.3-1.2	Brown
dryl	(0.2) 0.3 (0.5)	0.4-1.2	Brown
wetl	(0.2) 0.4 (0.5)	0.3-0.8	Brown
BRAC	(0.2) 0.4 (0.5)	0.6-1.5	Brown
GLOM	(0.6) 1.2 (2.2)	0-0.9	Whitish (brown)
GLOM	(1.0) 1.2 (2.0)	0-0.3	Whitish to light brown
HIRS	(0.7) 1.2 (2.0)	0-0.3	Whitish to light brown
GLAP	(0.9) 1.5 (2.0)	0-0.2	Whitish to light brown
PUMI	(0.6) 1.1 (2.2)	0.2-0.9	Light brown to brown
robu	(0.6) 0.8 (1.3)	0.2-0.9	Light brown to brown
sout	(1.0) 1.5 (2.2)	0.2-0.5	Light brown

in anther length and the marcescence of the anther are discussed in the following section.

The fruits are oblong to linear and are usually 2–3 mm long. Their size varies sufficiently with environmental conditions so as to be of little taxonomic value.

CHARACTER STATES

The measurements in TABLE 4 are based on herbarium specimens (primarily those of the author) and field observations covering the taxonomically useful

TABLE 4. **Character states** (*continued*).

	12	13	14	15	16
	Inflorescence				
Taxon	shape	orientation of branches	maximum branching	maximum branches	units/stem
ARCT	Oblong to ovate	Erect	1-3	1-5	(5) 16 (45)
GYRA	Linear to ovate	Erect	1-2	1-5	(2) 9 (31)
GYRA	Linear to ovate	Erect	1-2	1-5	(3) 9 (31)
comm	Linear to ovate	Erect	1-2	2-5	(3) 12 (31)
tenu	Linear	Erect	1-2	1-3	(3) 8 (13)
STEN	Linear	Erect	1-2	1-3	(2) 11 (26)
TRAC	Linear	Erect	1-2	1-2	(3) 8 (11)
LIEB	Linear to oblong	Erect	1-3	2-3	(1) 16 (50)
LIEB	Linear	Erect	1 (2)	1-2	(1) 4 (7)
PUNG	Linear to oblong	Erect	2-3	2-3	(7) 27 (50)
FLOR	Obla to obovate	Erect	2-3	2-5	(9) 51 (210)
LONG	Linear to oblong	Erect	2-3	2-4	(7) 45 (97)
VIRG	Linear to obpy	Erect or arching	2-4	2-6	(6) 62 (195)
VIRG	Linear to oblong	Erect	2-4	2-5	(6) 55 (175)
oldf	Linear to oblong	Erect	2-3	2-5	(6) 51 (150)
dece	Linear to oblong	Erect (arching)	2-4	2-4	(20) 82 (175)
smoo	Linear to obla	Erect	2-3	2-3	(12) 28 (60)
GLAU	Linear to obpy	Erect or arching	2-3	2-6	(19) 78 (190)
dryl	Linear to obpy	Erect or arching	2-3	2-3	(31) 84 (190)
wetl	Linear to oblong	Erect	2-3	2-6	(19) 72 (113)
BRAC	Ovate to obpy	Arching	2-3	3-5	(12) 75 (190)
GLOM	(Linear to) obpy	Erect	2-5	3-11	(10) 123 (600)
GLOM	Oblo to obpy	Erect	2-4	3-4	(25) 107 (200)
HIRS	(Linear to) oblong	Erect	2-4	4-5	(10) 96 (205)
GLAP	(Linear to) oblong	Erect	3-4	4-5	(30) 159 (400)
PUMI	Obla to obpy	Erect	2-5	3-11	(15) 132 (600)
robu	Obla to obpy	Erect	3-5	3-11	(28) 169 (600)
sout	Obla to obpy	Erect	2-3	3-7	(15) 95 (200)

morphological variation and the geographic range of the taxa. The sample size reflects the complexity of the taxa or (with *Andropogon liebmannii* var. *liebmannii* and the tenuous variant of *A. gyrans* var. *gyrans*) a low frequency of occurrence in nature. The first number for sample size in TABLE 4 is the total number of plants measured; the number of populations included in the measurements is in parentheses. For some taxa many plants have been measured for certain critical characters and fewer plants for other characters less important in distinguishing the taxa. Also, numerous herbarium specimens have been spot checked for many of the characters. For all quantitative measurements,

TABLE 4. **Character states** (*continued*).

	17	18	19	20
Taxon	Pubescence below raceme sheath	Raceme Sheath location	length (cm.)	width (mm.)
ARCT	0 to D	0	(3.3) 3.8-6.8 (9.0)	(2.5) 3.2-4.0 (5.0)
GYRA	0 to D	0,1	(3.5) 4.6-6.9 (13.5)	(1.5) 2.7-4.7 (8.0)
GYRA	0 to D	0,1	(3.5) 4.6-7.0 (13.5)	(1.5) 2.8-4.7 (8.0)
comm	(0 to) D	1 (0)	(3.5) 4.4-5.5 (13.5)	(2.0) 3.1-5.1 (8.0)
tenu	S to D	0	(4.0) 4.9-7.9 (9.5)	(1.5) 2.5-4.3 (5.0)
STEN	0 to D	0	(2.6) 4.2-6.6 (8.5)	(2.0) 2.8-4.8 (6.3)
TRAC	0 to D	0	(2.8) 4.1-5.8 (7.2)	(3.0) 4.0-4.7 (5.8)
LIEB	0 to D	0	(4.0) 4.9-7.4 (10.0)	(3.0) 4.2-6.1 (10.1)
LIEB	0 to S	0	(4.2) 4.7-7.0 (7.5)	(3.0) 3.2-4.2 (4.5)
PUNG	M to D	0	(4.0) 5.1-7.8 (10.0)	(4.1) 5.3-8.0 (10.1)
FLOR	0 to D	0	(3.0) 4.0-5.9 (7.0)	(1.5) 2.0-2.7 (3.6)
LONG	S to D	0	(2.5) 3.0-4.5 (6.0)	(2.5) 3.2-4.1 (5.5)
VIRG	0 to D	0	(2.1) 3.1-4.6 (6.7)	(1.7) 3.0-3.8 (5.6)
VIRG	0 to M	0	(2.2) 3.2-4.8 (6.7)	(1.7) 3.0-3.8 (5.6)
oldf	0 to S (M)	0	(2.3) 3.4-5.2 (6.7)	(2.2) 3.3-4.4 (5.6)
dece	(0) S to M	0	(2.2) 2.5-3.8 (4.5)	(1.7) 2.4-3.1 (4.0)
smoo	0 (S)	0	(2.8) 3.3-4.7 (6.7)	(3.0) 3.2-3.8 (5.2)
GLAU	0 to D	0	(2.1) 2.9-4.3 (6.0)	(2.7) 3.1-3.8 (5.5)
dryl	0	0	(2.1) 2.6-3.8 (4.9)	(2.7) 3.0-3.5 (4.5)
wetl	S to D	0	(2.4) 3.2-4.8 (6.0)	(2.7) 3.2-4.2 (5.5)
BRAC	(0 to) M	0	(2.1) 2.4-3.5 (4.1)	(2.3) 2.6-3.0 (3.8)
GLOM	S to D	0	(2.0) 2.9-4.4 (6.5)	(1.3) 2.3-3.1 (4.7)
GLOM	S to D	0	(2.5) 3.4-5.2 (6.5)	(2.0) 2.5-3.4 (4.7)
HIRS	(S) M to D	0	(2.5) 2.9-4.6 (5.7)	(2.0) 2.4-3.1 (4.0)
GLAP	(S) M to D	0	(2.0) 2.4-3.6 (4.4)	(1.3) 2.0-2.5 (3.0)
PUMI	S to D	0	(2.0) 2.9-4.4 (6.3)	(1.5) 2.1-2.9 (4.4)
robu	(S) M to D	0	(2.0) 2.9-4.3 (5.2)	(1.5) 2.0-2.5 (3.0)
sout	S to M	0	(2.3) 2.9-4.5 (6.3)	(1.5) 2.3-3.3 (4.4)

if two numbers are provided (characters 10, 14, 15, 22, 26, and 27) they represent the range of values recorded. Where three numbers are given (characters 1, 7–9, 16, 29, and 31), the first and last, which are enclosed in parentheses, indicate the range around the mean value. For four numbers (characters 19–21, 23, and 25) the first and last again indicate the range, while the two middle values represent the mean of the smallest and largest values recorded for all the plants. For all other characters, states enclosed in parentheses rarely occur in the taxon. If two states are given, they are both of intermediate

TABLE 4. **Character states** (*continued*).

	21	22	23
		Raceme	
Taxon	Peduncle length (mm.)	number	length (cm.)
ARCT	(9) 26-66 (115)	2 (3, 4)	(2.2) 2.6-4.3 (5.3)
GYRA	(1) 5-31 (195)	2-5	(1.5) 2.8-4.2 (5.5)
GYRA	(1) 5-42 (195)	2-5	(1.5) 2.6-3.9 (5.5)
comm	(4) 6-60 (195)	2-5	(1.5) 2.5-3.7 (5.5)
tenu	(1) 5-25 (50)	2-4	(2.3) 2.7-4.2 (5.5)
STEN	(3) 4-16 (45)	2 (3)	(2.5) 4.0-4.5 (6.0)
TRAC	(9) 14-31 (65)	2	(1.5) 2.4-3.6 (4.2)
LIEB	(10) 24-68 (130)	2-13	(2.0) 2.4-4.0 (5.0)
LIEB	(20) 32-88 (130)	2-9	(2.0) 2.5-4.1 (5.0)
PUNG	(10) 15-47 (70)	2-13	(2.0) 2.3-3.9 (4.7)
FLOR	(10) 19-48 (93)	2 (-4)	(2.0) 2.5-3.7 (4.5)
LONG	(1) 3-4 (13)	2 (3)	(1.3) 1.8-2.6 (4.0)
VIRG	(1) 4-6 (30)	2-7	(0.5) 1.7-2.8 (4.4)
VIRG	(1) 4-6 (30)	2-7	(0.5) 1.7-3.0 (4.4)
oldf	(2) 4-6 (12)	2-5 (-7)	(0.5) 1.9-3.3 (4.4)
dece	(1) 4-9 (30)	2 (3)	(1.3) 1.5-2.3 (3.0)
smoo	(2) 3-4 (6)	2-4 (-7)	(1.1) 1.5-2.9 (3.6)
GLAU	(2) 3-4 (10)	2 (3)	(1.4) 1.8-2.7 (4.0)
dryl	(2) 3-4 (5)	2	(1.4) 1.7-2.4 (3.2)
wetl	(2) 3-5 (10)	2 (3)	(1.5) 2.0-3.0 (4.0)
BRAC	(13) 20-31 (43)	2 (3)	(1.2) 1.5-2.1 (2.6)
GLOM	(1) 6-14 (60)	2 (-4)	(1.0) 1.7-2.5 (3.5)
GLOM	(4) 11-35 (60)	2 (-4)	(1.5) 2.1-2.9 (3.5)
HIRS	(2) 3-5 (8)	2	(1.3) 1.7-2.8 (3.3)
GLAP	(1) 2-4 (6)	2	(1.0) 1.3-2.0 (2.3)
PUMI	(2) 7-13 (40)	2 (-4)	(1.3) 1.8-2.4 (3.0)
robu	(2) 8-15 (40)	2	(1.3) 1.7-2.5 (3.0)
sout	(2) 5-10 (16)	2 (-4)	(1.7) 1.9-2.3 (2.8)

frequency (or both rare if in parentheses). For glaucousness (characters 2 and 3) "0" means absence and "1" presence. For stem glaucousness "1" further means that the glaucousness does not occur in the internode below about 2 cm under the node, and "2" indicates general occurrence of glaucousness in the internode. Absence or presence of sheath scabrousness (character 6) is shown with a "0" or a "1." In the pubescence-density characters (4 and 17) "0" is absence, "S" sparse, "M" moderate, and "D" dense. Pubescence orientation (character 5) is either appressed ("A"), spreading ("S"), or a combination of the two; when the leaves are always glabrous, this character is left blank.

TABLE 4. **Character states** (*continued*).

	24	25	26
	Rachis internode	Spikelet	
Taxon	pubescence	length (mm.)	width (mm.)
ARCT	0,1	(4.3) 4.9-5.4 (6.1)	0.7-1.0
GYRA	0	(3.0) 3.9-4.7 (5.7)	0.5-0.7
GYRA	0	(3.5) 4.1-4.5 (5.7)	0.5-0.7
comm	0	(3.5) 4.2-4.5 (5.7)	0.5-0.7
tenu	0	(3.5) 4.0-4.5 (5.2)	0.5-0.6
STEN	0	(3.0) 3.4-5.1 (5.5)	0.5-0.6
TRAC	0	(4.0) 4.8-5.0 (5.5)	0.6-0.8
LIEB	0	(3.0) 4.0-4.5 (6.0)	0.5-1.0
LIEB	0	(3.0) 3.4-3.9 (4.2)	0.5-0.9
PUNG	0	(4.3) 4.7-5.1 (6.9)	0.7-1.0
FLOR	1	(3.8) 4.4-4.8 (5.5)	0.5-0.7
LONG	0	(3.5) 4.1-4.5 (5.0)	0.5-0.8
VIRG	0	(2.6) 3.5-3.8 (4.7)	0.4-0.6
VIRG	0	(2.9) 3.5-3.8 (4.7)	0.4-0.6
oldf	0	(2.9) 3.7-3.9 (4.7)	0.4-0.6
dece	0	(3.0) 3.3-3.6 (4.0)	0.4-0.6
smoo	0	(3.0) 3.5-3.7 (4.2)	0.4-0.6
GLAU	0	(2.6) 3.4-3.7 (4.4)	0.4-0.5
dryl	0	(2.6) 3.2-3.5 (3.9)	0.4-0.5
wetl	0	(3.0) 3.5-3.9 (4.9)	0.4-0.5
BRAC	0	(4.1) 4.4-4.6 (5.0)	0.5-0.7
GLOM	0	(3.0) 3.7-4.0 (5.0)	0.4-0.6
GLOM	0	(3.8) 4.1-4.4 (5.0)	0.5-0.6
HIRS	0	(3.4) 3.6-3.8 (4.6)	0.4-0.6
GLAP	0	(3.0) 3.2-3.5 (3.8)	0.4-0.6
PUMI	0	(3.0) 3.8-4.1 (5.0)	0.4-0.6
robu	0	(3.0) 3.4-3.8 (4.5)	0.4-0.6
sout	0	(3.5) 4.2-4.5 (5.0)	0.4-0.6

Inflorescence shape (character 12) is linear, oblanceolate (abbreviated "obla"), oblong, ovate, obovate, or obpyramidal (abbreviated "obpy"). Raceme sheaths are located (character 18) so as to be either largely exposed ("0") or mostly hidden within enlarged stem sheaths ("1") after anthesis. Pubescence on the rachis internode (character 24) is either relatively sparse toward the base of the internode ("0") or uniformly distributed along the internode ("1"). Lower glume scabrousness (character 28) either occurs only above the middle of the glume ("0") or extends below the middle ("1"). Percent chasmogamy (character

TABLE 4. **Character states** (*continued*).

	27	28	29	30
			Awn	
Taxon	Maximum callus hair length (mm.)	Lower glume keel scabrousness	length (mm.)	base
ARCT	1.5-2.5	1	(0.5) 0.8 (1.6)	(0) 1
GYRA	1-5	0	(0.8) 1.8 (2.4)	0,1
GYRA	2-5	0	(1.3) 1.5 (2.2)	0,1
comm	2.5-4	0	(1.3) 1.8 (2.3)	(0) 1
tenu	2-5	0	(1.3) 2.0 (2.4)	(0) 1
STEN	1-2.5	0	(0.8) 1.5 (2.2)	0,1
TRAC	1.5-3.5	0	(1.1) 1.5 (2.3)	0,1
LIEB	1.5-2	0,1	(1.2) 1.8 (2.4)	1
LIEB	1.5-2	0	(1.2) 1.4 (1.6)	1
PUNG	1.5-2	0,1	(1.7) 2.1 (2.4)	1
FLOR	1-3	0	(0.5) 0.9 (1.5)	0
LONG	1.5-5	0	(1.0) 1.6 (2.1)	0,1
VIRG	1-3	0 (1)	(0.6) 1.4 (2.1)	0 (1)
VIRG	1-2.5	0 (1)	(0.8) 1.4 (2.0)	0
oldf	1-2.5	0 (1)	(1.0) 1.5 (2.0)	0
dece	1-2.5	0	(0.8) 1.2 (1.7)	0
smoo	1-1.5	0 (1)	(1.2) 1.5 (1.8)	0
GLAU	1-3	0	(0.6) 1.2 (2.1)	0 (1)
dryl	1-3	0	(0.6) 1.1 (1.5)	0 (1)
wetl	1-2.5	0	(0.9) 1.4 (2.1)	0 (1)
BRAC	1-1.5	0	(0.2) 0.7 (1.1)	0
GLOM	1-2.5	0,1	(0.6) 1.3 (1.9)	0 (1)
GLOM	1.5-2.5	0 (1)	(0.8) 1.2 (1.8)	1
HIRS	1-2	0 (1)	(1.0) 1.4 (1.7)	(0) 1
GLAP	1-2	0 (1)	(0.9) 1.2 (1.6)	(0) 1
PUMI	1-2.5	1	(0.6) 1.2 (1.9)	(0) 1
robu	1.5-2.5	1	(0.9) 1.4 (1.9)	(0) 1
sout	1-2	1	(0.6) 1.1 (1.7)	1

33), given as the mean (one standard error), is determined by looking for the presence (cleistogamy) or absence (chasmogamy) of a marcescent anther and stigmas in at least 30 postanthesis spikelets per plant.

TAXONOMIC TREATMENT

Taxonomic rank within the complex is based primarily on morphological distance between the taxa. Distances between the taxa have been determined

TABLE 4. **Character states** (*continued*).

	31	32	33
	Anther		
Taxon	length (mm.)	color	Mean percent chasmogamy ± S.E.
ARCT	(2.0) 2.5 (3.3)	Red	100 ± 0
GYRA	(0.6) 1.1 (1.4)	Yellow or purple	38 ± 3.3
GYRA	(0.7) 1.1 (1.4)	Yellow or purple	36 ± 4.7
comm	(0.9) 1.2 (1.4)	Yellow (purple)	38 ± 6.1
tenu	(0.7) 0.9 (1.2)	Yellow or purple	34 ± 5.2
STEN	(0.6) 1.2 (1.7)	Yellow	40 ± 6.5
TRAC	(1.2) 1.5 (2.0)	Yellow	98 ± 0.2
LIEB	(0.7) 1.2 (1.4)	Yellow	95 ± 1.2
LIEB	(1.1) 1.2 (1.4)	Yellow	98 ± 0.7
PUNG	(0.7) 1.1 (1.4)	Yellow	91 ± 2.2
FLOR	(1.3) 1.5 (2.0)	Yellow (purple)	98 ± 0.7
LONG	(0.9) 1.2 (1.6)	Yellow	84 ± 3.4
VIRG	(0.6) 0.9 (1.5)	Yellow or purple	64 ± 2.8
VIRG	(0.6) 0.8 (1.5)	Yellow or purple	60 ± 2.9
oldf	(0.6) 0.9 (1.2)	Yellow or purple	47 ± 5.9
dece	(0.6) 1.0 (1.5)	Yellow	88 ± 3.6
smoo	(0.6) 0.7 (1.0)	Purple	44 ± 4.8
GLAU	(0.7) 1.0 (1.2)	Yellow	70 ± 1.5
dryl	(0.9) 1.0 (1.5)	Yellow	97 ± 0.9
wetl	(0.7) 0.9 (1.1)	Yellow	42 ± 2.3
BRAC	(1.7) 2.1 (2.4)	Red	99 ± 0.01
GLOM	(0.5) 0.9 (1.5)	Yellow, red, or purple	66 ± 1.6
GLOM	(0.9) 1.2 (1.5)	Yellow	79 ± 3.4
HIRS	(0.7) 0.8 (1.1)	Yellow or purple	41 ± 3.2
GLAP	(0.5) 0.7 (0.9)	Yellow or purple	25 ± 2.9
PUMI	(0.7) 0.9 (1.1)	Yellow	93 ± 0.9
robu	(0.7) 0.9 (1.1)	Yellow	96 ± 0.6
sout	(0.8) 0.9 (1.0)	--	88 ± 1.9

through comparisons of the 33 characters (see TABLE 4) used in this study, assigning a value of "0" for no difference, "½" for intermediate overlap, and "1" for little or no overlap between the character states. (The rules for determining these values for each of the characters are presented in APPENDIX B.) The sum of these values for all the characters for any single pair of taxa is the distance between them (TABLES 5, 6). This distance represents the probability of misidentifying a specimen of one taxon as another taxon. The maximum distance between any pair of taxa is 21.5 (*Andropogon tracyi* and *A. glomeratus* var. *glaucopsis*), and the minimum between any of the lowest-ranking taxa

TABLE 5. **Morphological distance between the species.***

	ARCT	GYRA	TRAC	LIEB	FLOR	LONG	VIRG	BRAC	GLOM
ARCT									
GYRA	11								
TRAC	10	8							
LIEB	8	7	9.5						
FLOR	11.5	13	10.5	12					
LONG	11.5	7.5	9	12	12				
VIRG	12	9.5	12	12	9.5	6.5			
BRAC	13	17	16	17	9.5	14	9.5		
GLOM	15	13.5	14.5	12	10	12	8	13.5	

*For an explanation of how these distance values are determined, see the section on taxonomic rank and APPENDIX B.

(i.e., those that are not polytypic) is 3 (the old-field and smooth variants of *A. virginicus* var. *virginicus*). Any distance less than 6 is found only within species, and any greater than 9 occurs only between species.

In six of the thirty-six species pairs (TABLE 5), the distance is less than 9. In all of these cases, one or both of the species is polytypic. The character states of the polytypic taxa are the weighted mean or encompass the full range of variation of the subspecific taxa. This method of deriving character states of the polytypic taxa minimizes their distance from other taxa. The distances from the lowest-ranking taxa of a polytypic species to the lowest-ranking taxa of other species are generally greater than the distances separating the polytypic species (TABLE 6). Hence, in five of the six cases of species-to-species distances less than 9, most distances between the lowest-ranking taxa are at least 9. The one case in which most of the lowest-ranking taxa of the two species are separated by less than 9 is *Andropogon longiberbis* and *A. virginicus*. The reasons for maintaining these taxa as species are given in the discussion of *A. longiberbis*.

Morphological distance usually coincides with differences in ecological preferences or geographic distribution. More closely related taxa (e.g., *Andropogon glomeratus* vars. *hirsutior* and *glaucopsis*) may, however, have very similar ecological preferences and ranges.

"Taxon" is used here for a group of populations with similar morphological characteristics and ecological preferences. Only taxa separated by consistent and appreciable morphological gaps are recognized nomenclaturally. Nine of the taxa, here called variants, are not recognized formally because of the extreme difficulty in distinguishing between those belonging to the same variety. Apart from nomenclatural status, the variants are treated in the same fashion as species and varieties. The taxa are arranged in the taxonomic treatment so as to place those that are most closely related next to one another. Ambiguous names in the virginicus complex are discussed in APPENDIX C.

In the citation of herbarium specimens, abbreviations of the institutions follow the sixth edition of *Index Herbariorum* (Holmgren & Keuken, 1974). The herbaria and their abbreviations are listed in the acknowledgments.

Ordinarily, one specimen per county has been cited for taxa in the United States, and all specimens represented by a dot on the distribution maps have been cited for Mexico, Central America, the West Indies, and South America. Because the old-field variant of *Andropogon virginicus* var. *virginicus* and the robust variant of *A. glomeratus* var. *pumilus* are so abundant, only a representative number of counties from the United States have been cited.

It is important to read the section on morphology in relation to taxonomy before using the keys. All characters concerning the leaves are based on healthy, nonsenescent leaves at the second to fourth nodes above the base of the plant. All characters concerning the dispersal units are based on units near the middle of the raceme.

KEY TO THE SPECIES OF THE VIRGINICUS COMPLEX

1. Postflowering peduncles less than 10 mm long.
   2. Plants small—stems usually less than 1 m tall, leaves usually less than 3 mm wide, inflorescence branching of first or second order only, inflorescence units less than 30 per stem; raceme sheaths usually more than 4.6 cm long. .... 2. *Andropogon gyrans.*
   2. Plants larger—stems usually more than 1 m tall, leaves usually more than 3 mm wide, inflorescence branching of second or higher order, inflorescence units more than 30 per stem; raceme sheaths usually less than 4.6 cm long.
      3. Spikelets more than 4 mm long; leaf pubescence appressed (rarely spreading); longest callus hairs often more than 2.5 mm long. .... 6. *Andropogon longiberbis.*
      3. Spikelets usually less than 4 mm long; leaf pubescence spreading (rarely appressed); longest callus hairs less than 2.5 mm long.
         4. Leaves usually over 37 cm long; stem sheaths often scabrous; ligules usually more than 1 mm long (if less than 1 mm, then keels of lower glume of spikelets often scabrous to below middle). .. 9. *Andropogon glomeratus.*
         4. Leaves usually less than 31 cm long; stem sheaths smooth (very rarely somewhat scabrous); ligules less than 1 mm long; keels of lower glume scabrous only above middle. .... 7. *Andropogon virginicus.*
1. One or more postflowering peduncles more than 15 mm long.
   5. Inflorescence units with (2 to) 4 to 6 (to 13) racemes. .... 4. *Andropogon liebmannii.*
   5. Inflorescence units usually with 2 racemes, occasionally with 3 or more.
      6. Plants small—stems usually less than 1 m tall, leaves usually less than 3 mm wide, inflorescence branching of first or second order only, inflorescence units less than 30 per stem.
         7. Spikelets (4–)4.8–5(–5.5) by 0.6–0.8 mm; racemes in twos; anthers more than 1.2 mm long. .... 3. *Andropogon tracyi.*
         7. Spikelets (3.5–)4–4.5(–5.2) by 0.5–0.6 mm; racemes often more than 2 per inflorescence unit; anthers less than 1.2 mm long. .. 2. *Andropogon gyrans.*
      6. Plants larger—stems usually more than 1 m tall, leaves usually more than 3

TABLE 6. **Morphological distance between the taxa.**

	ARCT	GYRA	GYRA	comm	tenu	STEN	TRAC	LIEB	LIEB	PUNG	FLOR	LONG	VIRG	VIRG	oldf	dece	smoo	GLAU	dryl	wetl	BRAC	GLOM	GLOM	HIRS	GLAP	PUMI	robu	sout
ARCT																												
GYRA	11																											
GYRA	12.*	0																										
comm	11.	2.	1																									
tenu	12.	2	2	4																								
STEN	12	6	5.	5	5																							
TRAC	10	8	7	9.	10	6.																						
LIEB	8	7	7.	8.	9.	6	9.																					
LIEB	11.	8	8.	10	9.	7.	10	4.																				
PUNG	9.	9.	9.	11	11.	10	11	2	9																			
FLOR	11.	13	13.	13.	17.	14	10.	12	16	13																		
LONG	11.	7.	8	8	10.	10	9	12	14.	13.	12																	
VIRG	12	9.	9.	10.	10.	12	12	12	14	13.	9.	6.																
VIRG	13.	8	10	11	9	10	11.	12.	13	14.	9.	6.	1.															
oldf	13	9	11	10.	11	11	11	12	12.	15	11.	7	3.	2														
dece	14	14	14	14	17	11	14.	13.	14.	13	10	6.	4	4	4.													
smoo	15	10	10.	12	13	15	16.	15.	15.	17	12.	11	3	2	3	7.												
GLAU	13.	13.	14	14.	15	11	13	16	17.	17	12.	8	2	2.	5	5	4.											
dryl	15	16	16	16	15	13.	14	17	18.	17	13.	10	3.	5	8.	5.	5.	0.										
wetl	14.	12	13.	12	16	12	12.	16.	18	17.	12.	7.	3.	2.	4	6	4.	1.	4									
BRAC	13	17	17.	19	20.	17	16	17	19.	16.	9.	14	9.	10.	12.	8	14.	12	13	14.								
GLOM	15	13.	14	13.	16	12	14.	12	15.	13	10	12	8	8	11	10.	10	9.	12	10	13.							
GLOM	12	11.	12.	11.	14.	12	14.	8.	13	11	10.	9	10.	9.	11.	9	14	12	14.	12.	13	3						
HIRS	15	13	15.	14	16	14	19.	12.	15.	12.	13.	11	8.	7	9	7.	11.	11.	14.	11	14	3	4					
GLAP	18	17	17	19.	17	15.	21.	16.	19	17.	15.	16.	10	9.	11.	11	11.	10	11.	10.	16	8	9	6.				
PUMI	13	14	14.	14.	16	12.	15.	11.	15.	12	9.	11.	9	9.	12.	8	13	11.	13	11.	12	2	4.	5.	8.			
robu	13	15.	15	14	16.	13.	16	12	13.	11.	10	13	9.	10	12.	8	13	12	13	12	13	4.	6	6.	9	1.		
sout	12	12.	12.	14	15.	12.	16.	13.	17.	14.	11	8.	9	8.	9.	9	12.	11	13.	11.	12	4	5	5	9	4	6	

*The decimal point following a distance value indicates that the value should be increased by 0.5 (e.g., 12. = 12.5).

mm wide, inflorescence branching of second or higher order, inflorescence units more than 30 per stem.

8. Racemes usually less than 2.1(–2.6) cm long; inflorescence branches long and arching, inflorescence open, loose. . . 8. *Andropogon brachystachyus.*
8. Racemes usually longer than 2 cm; inflorescence branches mostly erect, inflorescence more or less dense.
   9. Rachis internodes densely pubescent over entire length; spikelets usually more than 4.4 mm long; awns usually less than 1 cm long; anthers usually more than 1.5 mm long.
      10. Leaves (32–)42(–61) cm long, glabrous; stem sheaths often scabrous; inflorescence units (9 to) 51 (to 210) per stem; anthers less than 2 mm long. .... 5. *Andropogon floridanus.*
      10. Leaves (15–)21(–35) cm long, often pubescent; stem sheaths smooth; inflorescence units (9 to) 16 (to 45) per stem; anthers more than 2 mm long. .... 1. *Andropogon arctatus.*
   9. Rachis internodes sparsely pubescent toward base; spikelets usually less than 4.4 mm long; awns usually more than 1 mm long; anthers less than 1.5 mm long.
      11. Leaves usually over 37 cm long; stem sheaths often scabrous; ligules usually more than 1 mm long (if less than 1 mm, then keels of lower glume of spikelets often scabrous to below middle). .... 9. *Andropogon glomeratus.*
      11. Leaves usually less than 31 cm long; stem sheaths smooth (very rarely somewhat scabrous); ligules less than 1 mm long; keels of lower glume scabrous only above middle. .... 7. *Andropogon virginicus.*

Key to the Taxa of the Virginicus Complex and Andropogon ternarius

1. Postflowering peduncles less than 10 mm long.
   2. Leaves strongly glaucous, especially when young.
      3. Ligules (0.9–)1.5(–2) mm long, with ciliations less than 0.3 mm long; leaf blades usually more than 35 cm long; racemes (1–)1.3–2(–2.3) cm long; pubescence below raceme sheath moderate to dense. .... 9c. *A. glomeratus* var. *glaucopsis.*
      3. Ligules (0.2–)0.4(–0.5) mm long, with ciliations more than 0.3 mm long; leaf blades usually less than 35 cm long; racemes (1.4–)1.8–2.7(–4) cm long (if less than 2 cm, then pubescence below raceme sheath usually absent or sparse).
         4. Pubescence below raceme sheaths absent; raceme sheaths (2.1–)2.6–3.8(–4.9) cm long; racemes (1.4–)1.7–2.4(–3.2) cm long; spikelets (2.6–)3.4–3.7(–4.4) mm long; plants of well-drained soils on Coastal Plain from southern Virginia to southern Alabama. .... 7b. 1. Drylands variant of *A. virginicus* var. *glaucus.*
         4. Pubescence below raceme sheath sparse to dense; raceme sheaths (2.4–)3.2–4.8(–6) cm long; racemes (1.5–)2–3(–4) cm long; spikelets (3–)3.5–3.9(–4.9) mm long; plants of poorly drained soils on Coastal Plain from southern New Jersey to eastern Texas. .... 7b. 2. Wetlands variant of *A. virginicus* var. *glaucus.*
   2. Leaves green (sometimes slightly glaucous in *A. gyrans* var. *stenophyllus* and smooth variant of *A. virginicus* var. *virginicus*).
      5. Stem sheaths scabrous with upwardly directed prickle hairs; leaf blades usually more than 35 cm long.
         6. Ligules usually less than 1 mm long; raceme sheaths usually less than 2.5 mm wide; keels of lower glume often scabrous below middle. .... 9d. 1. Robust variant of *A. glomeratus* var. *pumilus.*

6. Ligules usually more than 1 mm long; raceme sheaths mostly more than 2.5 mm wide; keels of lower glume glabrous or scabrous below middle only in southwestern variant of *A. glomeratus* var. *pumilus*.
   7. Keels of lower glume rarely scabrous below middle; plants of eastern United States.
      8. Inflorescences (linear to) oblong; spikelets usually less than 4 mm long; anthers usually marcescent within spikelets; peduncles less than 10 mm long; plants of Coastal Plain from southern Virginia to southern Mississippi. . . . . 9b. *A. glomeratus* var. *hirsutior*.
      8. Inflorescences oblong to obpyramidal; spikelets usually more than 4 mm long; anthers usually not marcescent within spikelet; usually some mature peduncles more than 10 mm long; plants ranging from Massachusetts to southern Mississippi on Coastal Plain and well inland. . . . . 9a. *A. glomeratus* var. *glomeratus*.
   7. Keels of lower glume usually scabrous below middle; plants of southwestern United States. . . . . 9d. 2. Southwestern variant of *A. glomeratus* var. *pumilus*.

5. Stem sheaths smooth, very rarely scabrous; leaf blades usually less than 35 cm long (except in robust variant of *A. glomeratus* var. *pumilus*).
   9. Inflorescence units largely hidden within broadened, strongly overlapping uppermost stem sheaths. . . . . 2a. 1. Common variant of *A. gyrans* var. *gyrans*.
   9. Inflorescence units mostly exposed at maturity.
      10. Leaves glabrous.
          11. Ligules (0.8–)1.1(–1.5) mm long, with ciliations less than 0.1 mm long; basal leaves often filiform, less than 1.5 mm wide, strongly erect. . . . . 2b. *A. gyrans* var. *stenophyllus*.
          11. Ligules less than 0.7 mm long (rarely to 1 mm, but usually longer in southwestern variant of *A. glomeratus* var. *pumilus*), with ciliations usually greater than 0.1 mm long; basal leaves usually more than 2 mm wide, soon arching.
              12. Stem internodes glaucous; some inflorescence units (especially at stem and branch apices) with 3 or more racemes.
                  13. Stems less than 1 m long; inflorescence units less than 14 per stem; spikelets usually more than 4 mm long. . . . . 2a. 2. Tenuous variant of *A. gyrans* var. *gyrans*.
                  13. Stems more than 1 m long; inflorescence units usually more than 14 per stem; spikelets usually less than 4 mm long. . . . . 7a. 3. Smooth variant of *A. virginicus* var. *virginicus*.
              12. Stem internodes green, or glaucous just below node only; inflorescence units with 2 racemes (infrequently more).
                  14. Ligules more than 1 mm long; keels of lower glume often scabrous to below middle; spikelets usually greater than 4 mm long; plants of southwestern United States and northwestern Mexico. . . . . 9d. 2. Southwestern variant of *A. glomeratus* var. *pumilus*.
                  14. Ligules less than 1 mm long; keels of lower glume scabrous only above middle; spikelets less than 4 mm long; plants of southeastern United States. . . . . 7a. 2. Deceptive variant of *A. virginicus* var. *virginicus*.
      10. Leaves pubescent, at least on margin near collar.
          15. Keels of lower glume often scabrous below middle; leaves usually more than 44 cm long.

16. Spikelets usually less than 4 mm long; ligules (0.6–)0.8(–1.3) mm long; raceme sheaths usually less than 2.5 mm wide; wide-ranging plants of most of temperate North and Central America except southwestern United States. . . . . 9d. 1. Robust variant of *A. glomeratus* var. *pumilus.*
16. Spikelets usually longer than 4 mm; ligules (1–)1.5(–2.2) mm long; raceme sheaths usually more than 2.5 mm wide; plants of southwestern United States and northwestern Mexico. . . . . 9d. 2. Southwestern variant of *A. glomeratus* var. *pumilus.*

15. Keels of lower glume scabrous only above middle; leaves usually less than 31 cm long.
17. Pubescence of young stem sheaths appressed; spikelets usually more than 4 mm long; hairs on rachis internode and pedicel dense, long. . . . . 6. *A. longiberbis.*
17. Pubescence of young stem sheaths spreading; spikelets mostly less than 4 mm long; hairs on rachis internode and pedicel rather sparse, short.
18. Raceme sheaths (2.7–)3.3–4.4(–5.5) mm wide; racemes often more than 2 per inflorescence unit; widespread through most of eastern United States, absent from all but southernmost Florida. . . . . 7a. 1. Old-field variant of *A. virginicus* var. *virginicus.*
18. Raceme sheaths (1.7–)2.4–3.1(–4) mm wide; racemes usually 2 per inflorescence unit; Coastal Plain from Florida to southern Virginia, common only in Florida. . . . . 7a. 2. Deceptive variant of *A. virginicus* var. *virginicus.*

1. One or more postflowering peduncles more than 15 mm long.
19. All raceme sheaths largely hidden before senescence within broadened, strongly overlapping, uppermost stem sheaths. . . . . 2a. 1. Common variant of *A. gyrans* var. *gyrans.*
19. Most or all raceme sheaths clearly exposed after anthesis; uppermost stem sheaths reduced, not strongly overlapping.
20. Inflorescence units with (2 to) 4 to 6 (to 13) racemes.
21. Stems less than 0.9 m tall; leaves less than 15 cm long; stem sheaths more or less glabrous (to densely pubescent); spikelets less than 4.2 mm long; plants of Mexico. . . . . 4a. *A. liebmannii* var. *liebmannii.*
21. Stems more than 0.8 m tall; leaves more than 15 cm long; stem sheaths usually densely woolly-pubescent, at least near collar; spikelets more than 4.2 mm long; plants of United States. . . . . 4b. *A. liebmannii* var. *pungensis.*
20. Inflorescence units with 2 (or more) racemes.
22. Stem sheaths scabrous with upwardly directed prickle hairs.
23. Rachis internodes becoming sparsely pubescent toward base; stem sheaths usually more or less pubescent; plants of moist or disturbed ground.
24. Ligules (1–)1.2(–2) mm long, with ciliations less than 0.3 mm long; keels of lower glume scabrous only above middle. . . . . 9a. *A. glomeratus* var. *glomeratus.*
24. Ligules (0.6–)0.8(–1.3) mm long, with ciliations 0.2–0.9 mm long; keels of lower glume often scabrous below middle. . . . . 9d. 1. Robust variant of *A. glomeratus* var. *pumilus.*
23. Rachis internodes densely and uniformly pubescent, not becoming

sparsely pubescent toward base; stem sheaths rarely pubescent; plants of sandy uplands. .... 5. *A. floridanus.*

22. Stem sheaths smooth.
    25. Many or all peduncles longer than raceme sheaths at maturity, racemes then fully exserted above apex of raceme sheath.
        26. Racemes usually less than 2.1(–2.6) cm long; inflorescence branches long and arching, inflorescences open, loose. .... 8. *A. brachystachyus.*
        26. Racemes exceeding 2 cm in length, usually more than 2.5 cm long; inflorescence branches erect, inflorescences more or less dense.
            27. Stems less than 0.9 m tall; leaves less than 2 mm wide; some racemes usually fully included within raceme sheaths at maturity on peduncles less than 10 mm long; anthers often marcescent. .... 2a. 2. Tenuous variant of *A. gyrans* var. *gyrans.*
            27. Stems usually more than 1 m tall; leaves mostly more than 3 mm wide; racemes rarely included within raceme sheaths at maturity, peduncles rarely less than 15 mm long; anthers rarely marcescent.
                28. Leaves glabrous, blade mostly more than 35 cm long; stamen 1 per flower, anther less than 2 mm long. .. .. 5. *A. floridanus.*
                28. Leaves often pubescent, blade less than 35 cm long; stamens 3 per flower (if only 1, anther more than 2 mm long).
                    29. Stamen(s) mostly 1; lower glumes more or less folded; awns less than 1 cm long. .... 1. *A. arctatus.*
                    29. Stamens 3; lower glumes flat; awns more than 1 cm long.
                        30. Lower glume nerved between keels (most easily seen on adaxial surface); endemic of Florida. .... *A. ternarius* var. *cabanisii.*
                        30. Lower glume not nerved between keels; widespread through most of eastern United States. .... *A. ternarius* var. *ternarius.*
    25. Peduncles all shorter than raceme sheaths, at least bases of racemes not fully exserted above raceme sheath apices.
        31. Stems less than 1.2 m tall; leaf blades less than 30 cm by 3 mm; inflorescence units rarely more than 20 per stem.
            32. Raceme sheaths (2.2–)2.5–3.8(–4.5) cm long; spikelets usually less than 4 mm long. .... 7a. 2. Deceptive variant of *A. virginicus* var. *virginicus.*
            32. Raceme sheaths usually more than 4 cm long; spikelets generally more than 4 mm long.
                33. Ligules more than 0.8 mm long, with ciliations less than 0.1 mm long; plants of bogs and ditches. .... 2b. *A. gyrans* var. *stenophyllus.*
                33. Ligules less than 0.8 mm long, with ciliations often more than 0.2 mm long; plants of well-drained soils.
                    34. Spikelets (4–)4.8–5(–5.5) by 0.6–0.8 mm; racemes paired; anthers more than 1.2 mm long. .... 3. *A. tracyi.*

34. Spikelets (3.5–)4–4.5(–5.2) by 0.5–0.6 mm; racemes 2 to 4 per inflorescence unit; anthers less than 1.2 mm long. .... 2a. 2. Tenuous variant of *A. gyrans* var. *gyrans.*

31. Stems usually more than 1.2 m tall; leaf blades often more than 30 cm by 3 mm; inflorescence units usually more than 20 per stem.

35. Racemes usually less than 2.1(–2.6) cm long; inflorescence branches long and arching, inflorescences open, loose. .... 8. *A. brachystachyus.*

35. Racemes often longer than 2 cm; inflorescence branches erect (infrequently somewhat spreading in deceptive variant of *A. virginicus* var. *virginicus*), inflorescences more or less dense.

36. Rachis internodes densely and uniformly pubescent, not becoming sparsely hairy toward base; many peduncles regularly more than 30 mm long. .... 5. *A. floridanus.*

36. Rachis internodes sparsely pubescent toward base; peduncles rarely more than 20 mm long.

37. Raceme sheaths (1.5–)2–2.5(–3) mm wide; keels of lower glume often scabrous below middle; stems to 2.5 m tall; leaves to 109 cm by 9.5 mm. .... 9d. 1. Robust variant of *A. glomeratus* var. *pumilus.*

37. Raceme sheaths (1.7–)2.4–3.1(–4) mm wide; keels of lower glume scabrous only above middle; stems less than 1.7 m tall; leaves less than 35 cm by 5.5 mm. .... 7a. 1. Deceptive variant of *A. virginicus* var. *virginicus.*

1. **Andropogon arctatus** Chapman, Bot. Gaz. **3:** 20. 1878. Based on *Andropogon tetrastachyus* Ell. var. *distachyus* Chapman, Fl. So. U. S. 581. 1860. Not *Andropogon distachyus* L., 1753. TYPE:[2] Florida, *Chapman s.n.* (lectotype, NY!). FIGURES 11, K; 34.

Sorghum arctatum (Chapman) Kuntze, Rev. Gen. Pl. **2:** 791. 1891.
Leptopogon carinatus (Nees) G. Roberty subvar. *arctatus* (Chapman) G. Roberty, Boissiera **9:** 197. 1960.

DIAGNOSIS. Inflorescence units averaging 16 per stem; peduncles all long; spikelets long and wide, the lower glume more or less concave at maturity, with keels scabrous to below middle; anthers long, red; flowers rarely, if ever, chasmogamous.

DISTRIBUTION. Flatwoods, bogs, and scrublands. Florida (except extreme south and Suwannee River drainage) and southern Alabama (MAP 5).

REPRESENTATIVE SPECIMENS. **United States.** FLORIDA: Bay, *Godfrey 76774* (FSU); Brevard, *Fredholm 6110* (US); Calhoun, *Woods s.n.*, 1954 (TENN); Charlotte, *Lewis 107* (US); Clay, *Swallen 5584* (US); Collier, *Lakela 31145* (DUKE); Escambia, *Campbell 3944*; Franklin, *Hausman s.n.*, 1867 (NY); Gulf, *Silveus 6735-A* (TAES); Highlands, *Campbell 4118* (GH); Hillsborough, *Shuey 1507* (USF); Jackson, *Godfrey et al. 76736* (FSU); Liberty, *Godfrey*

[2]A Chapman specimen from NY, annotated in his script, is here designated the lectotype.

FIGURES 29–35. 29–31, *Andropogon gyrans* var. *gyrans*, inflorescences: 29, common variant (*Campbell 4143*), from one population, showing variation from mostly cleistogamous (left) to mostly chasmogamous (right) flowering; 30, common variant (*Campbell 4095*), senescent; 31, tenuous variant, showing plants with predominantlv cleistogamous (left, *Campbell 3746*) and mostly chasmogamous (*Campbell 3873*) flowers. 32, 33, *A.*

74577 (FSU, NCU, VDB); Manatee, *Simpson s.n.*, 1889 (GH); Osceola, *Ray et al. 10490* (GH, US, USF); Santa Rosa, *Combs 486* (US); Walton, *A. H. Curtiss 6924* (GH, MO, US); Washington, *Combs 661* (US). ALABAMA: Covington, *Kral 44769* (GH, VDB).

Andropogon arctatus is unique in the virginicus complex in four respects. First, it does not grow in the Suwannee straits, a corridor along the Suwannee River from the Okefenokee Swamp in southern Georgia to the Gulf of Mexico. The distribution of other members of the virginicus complex that are common in Florida includes the Suwannee straits.

Second, it appears to have a life history different from that of the successful colonizing taxa of the virginicus complex. The six densest populations of this taxon observed in my field studies grew in recently burned areas. Three of these were clear-cut slash pine (*Pinus elliottii* Engelmann) timberlands in northwestern Florida, where fire is routinely used by the forestry industry in site preparation. One of these localities, in Liberty County, was observed by Dr. Robert K. Godfrey in 1976; the following year there were only a few individuals where there had previously been hundreds. The same marked reduction in the number of flowering plants occurred in the other two "pine fields" in the second year after site preparation. In one of these localities, numerous basal clumps of leaves of this species were found in the third year. It appears that *Andropogon arctatus* remains in this vegetative state until it is burned, then flowers abundantly before returning to a vegetative state. Restriction of flowering to a year or two following fire probably accounts in large part for the supposed rarity of this taxon. (Removal of the forest canopy by heavy winds or lumbering operations may, in certain circumstances, also stimulate flowering.) Although other andropogons are stimulated by fire (FIGURE 26), the number of their flowering stems tends to increase greatly two and three years later. Also, the other andropogons infect a burned site with dispersal units from nearby populations rather than remaining in situ until fire occurs.

Third, in contrast to the mostly cespitose habit of the rest of the virginicus complex, the base of the plant of *Andropogon arctatus* is a short, rather thick rhizome.

Fourth, the anthers of *Andropogon arctatus* are longer than those of any other taxon in the virginicus complex: the lower limit of the range of *A. arctatus* overlaps the upper limit of that of only *A. brachystachyus*. Although the flowers of *A. arctatus* usually have one stamen, out of 138 flowers from six individual plants in one population in Liberty County, Florida (*Campbell 4060*), 68 percent had one stamen, 29 percent two, and 3 percent three. In the virginicus complex as a whole, the frequency of two- and three-stamened flowers is less than 0.1 percent. In addition to stamen number and anther length, other features associated with chasmogamy—long peduncles and large spikelets—point to the relatively primitive position of *A. arctatus* in the virginicus complex.

In overall aspect *Andropogon arctatus* closely resembles *A. ternarius*, which is the only other common United States species in sect. LEPTOPOGON outside the virginicus complex. *Andropogon ternarius*, however, is an unlikely ancestor

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gyrans var. *stenophyllus* (*Campbell 3813*): 32, two stems; 33, basal leaves. 34, *A. arctatus* (*Campbell 3944*), inflorescence. 35, *A. tracyi* (*Campbell 4100*), stem. Scale = 15 cm.

of *A. arctatus* because it is tetraploid. *Andropogon ternarius* var. *cabanisii* (Hackel) Fern. & Griscom (chromosome number unknown) differs from *A. arctatus* only in stamen number and in the size and intercarinal nerves of the lower glumes. Knowledge of the chromosome number of *A. ternarius* var. *cabanisii* is necessary to clarify its relationship to *A. arctatus.*

The closest relatives of *Andropogon arctatus* in the virginicus complex are probably *A. floridanus* and the common variant of *A. gyrans* var. *gyrans.* All three taxa may produce very long peduncled racemes that are more or less densely pubescent with whitish hairs.

2. **Andropogon gyrans** Ashe, Jour. Elisha Mitchell Sci. Soc. **15:** 113. 1898. NEOTYPE: North Carolina, Wake or Orange County, *Ashe 2034,* 1896 (NCU!).

DIAGNOSIS. Stems short; leaves narrow; inflorescences little branched and bearing few inflorescence units; raceme sheaths long and wide; peduncles all short or short and long on same plant; racemes long; callus hairs long (except taxon 2b).

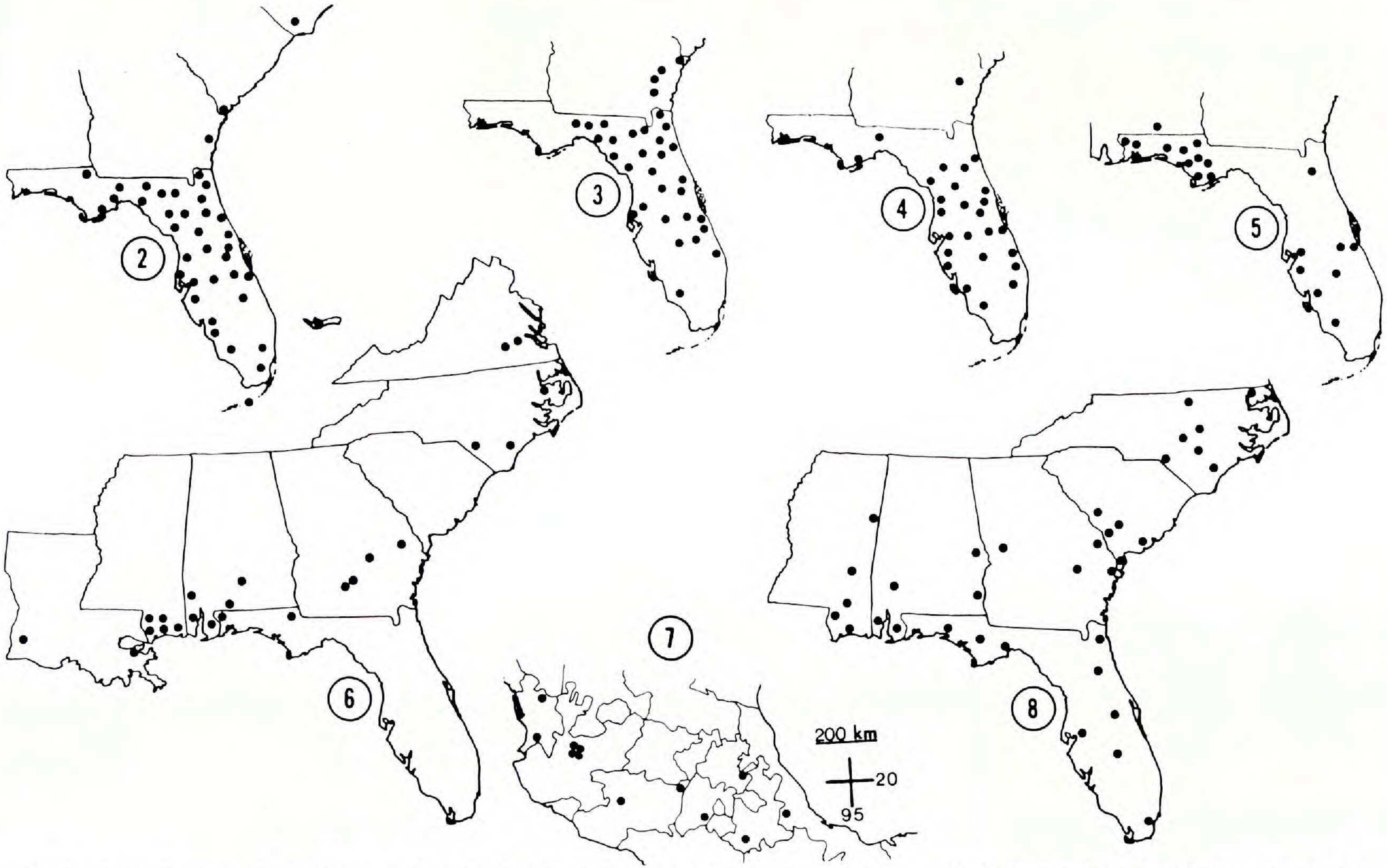
DISTRIBUTION. Dry or wet soils. New Jersey to Missouri, south to Florida and Texas; rare in Central America and West Indies.

This common and widespread taxon has long been known as *Andropogon elliottii* Chapman. Chapman published this name (Fl. So. U. S. 581. 1860) as new for *A. argenteus* Ell. (Bot. S. Carolina Georgia **1:** 148. 1816), a later homonym of *A. argenteus* DC. (1813). Elliott's description and type (Scribner, 1901), however, clearly place this name in synonymy with *A. ternarius* Michaux (1803). The synonymy of *A. ternarius* is presented in APPENDIX D.

The next oldest name at the species level is *Andropogon clandestinus* Wood, a later homonym of *A. clandestinus* Nees (see synonymy under taxon 2a below). The next available name is *A. gyrans.*

The specimen chosen as the neotype matches Ashe's protologue in most respects. The stems on this sheet fit his description in stem height, leaf-sheath glabrousness, and raceme number. The specimen label bears, in Ashe's script, the following information: "*Andropogon.* On sandstone between [?] and Chapel Hill, N.C. Wake or Orange Co. No. 2034 Date Oct 1896 Coll. W.W. Ashe." At the end of his protologue, Ashe stated "collected by the writer in pine woods in Durham county, N.C., Oct. 1896." It should be noted that Wake and Orange counties lie on either side of Durham County. It may well be that this specimen was the basis for Ashe's *Andropogon gyrans* and that the discrepancies of label and protologue are due to his carelessness. This specimen cannot, however, be definitely tied to Ashe's name and so is designated as neotype.

The equivalence of Ashe's specimen to the widespread taxon long known as *Andropogon elliottii* is questionable. The upper stem sheaths of this species are usually conspicuously overlapping and inflated, a distinctive and unique feature; those of the neotype are remote and not inflated. Less striking characters (short stems, dense hairs at the base of the raceme sheaths, number of racemes per inflorescence unit, long callus hairs, and twisting of the bases of the awns), however, clearly equate the neotype with the widespread taxon. This specimen



MAPS 2–8. Distributions: 2, *Andropogon longiberbis*; 3, *A. brachystachyus*; 4, *A. floridanus*; 5, *A. arctatus*; 6, *A. liebmannii* var. *pungensis*; 7, *A. liebmannii* var. *liebmannii* (central Mexico); 8, *A. tracyi*.

and a few others from throughout the Coastal Plain of the southeastern United States are intermediate between the common and tenuous variants of *A. gyrans* var. *gyrans*; they appear to be plants of the common variant in which overlapping and inflation of the upper stem sheaths are not strongly expressed.

There are two clusters of characters uniting the three taxa of this species. First, they are all small plants with small inflorescences, but the inflorescence unit and many of its parts are larger than those of most other taxa. This contrast of sizes provides a quick means of distinguishing these three taxa from depauperate individuals of *Andropogon virginicus*. Second, the other broomsedges have either all short peduncles, all long peduncles, or more or less continuous variation from short to long within a single plant. Variation is bimodal on an individual in the common variant of *A. gyrans* var. *gyrans*, or between individuals in the tenuous variant and *A. gyrans* var. *stenophyllus*, since some have only short peduncles and some mostly long peduncles. Occasionally, short- and long-peduncled plants of these two taxa occur in the same population, but more often they are separated in different populations. This bimodality reflects a variability that tends to correspond to ecological and geographic differences.

Hackel's subvar. *stenophyllus* is here made a variety of *Andropogon gyrans* for the first time. In addition to the characters uniting this taxon to the common and tenuous variants of var. *gyrans* discussed above, var. *stenophyllus* is separated from these two variants by a distance of 5 (TABLE 6).

Key to the Subspecific Taxa of *Andropogon gyrans*

1. Ligules usually less than 0.8 mm long; plants of well-drained soils, rarely of poorly drained sites.
   2. Raceme sheaths usually hidden within inflated, strongly overlapping upper stem sheaths. .... 2a. 1. Common variant of *A. gyrans* var. *gyrans*.
   2. Raceme sheaths mostly visible. .... 2a. 2. Tenuous variant of *A. gyrans* var. *gyrans*.
1. Ligules (0.8–)1.1(–1.5) mm long; plants of bogs and ditches. .... 2b. *A. gyrans* var. *stenophyllus*.

2a. **Andropogon gyrans** Ashe var. **gyrans**

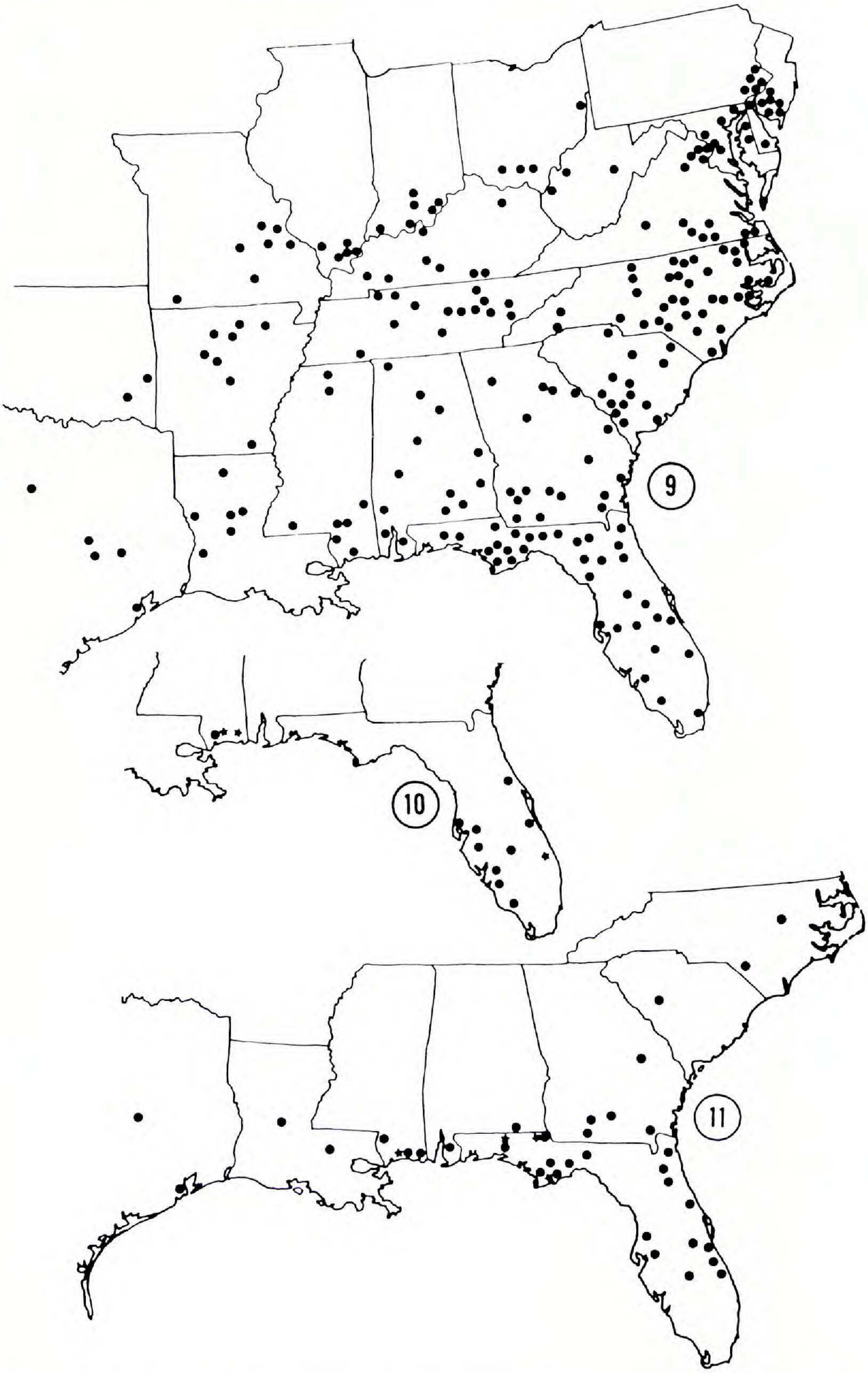
Andropogon clandestinus Wood, Class-book Bot. 809. 1861, *ex char.* (as *clandestina*). Not *Andropogon clandestinus* Nees, 1854. TYPE: unknown.

Andropogon elliotti Chapman var. *gracilior* Hackel in DC. Monogr. Phanerog. **6:** 415. 1889. TYPE: Florida, Duval County, *A. H. Curtiss 3636a* (holotype, not seen; isotypes, DUKE!, FSU!, GA!, GH!, MICH!, MISSA!, MO (two sheets)!, NCU!, US!). *Andropogon gracilior* (Hackel) Nash in Small, Fl. SE. U. S. 63. 1903. *Andropogon elliottii* Chapman f. *gracilior* (Hackel) Blomq. Grasses N. Carolina, 203. 1948.

Andropogon campyloracheus Nash, Bull. New York Bot. Gard. **1:** 431. 1900. Based on *Andropogon elliottii* Chapman var. *laxiflorus* Scribner, Bull. Torrey Bot. Club **23:** 146. 1896. Not *Andropogon laxiflorus* Steudel, 1854. TYPE: Florida, Lake County, *Nash 1738*, 1894 (holotype, US!; isotypes, GH!, MICH!). *Anatherum virginicum* (L.) subvar. *laxiflorum* (Scribner) G. Roberty, Boissiera **9:** 213. 1960.

Andropogon subtenuis Nash in Small, Fl. SE. U. S. 63, 64. 1903. TYPE: Mississippi, Harrison County, *Tracy 2243*, 1896 (holotype, NY!).

Andropogon virginicus L. var. *graciliformis* León, Bull. Torrey Bot. Club **53:** 457. 1926.



MAPS 9–11. Distribution of *Andropogon gyrans*: 9, var. *gyrans*, common variant (also outside United States; see representative specimens); 10, var. *gyrans*, tenuous variant; 11, var. *stenophyllus*. (In 10 and 11 dots represent populations of plants with short peduncles; stars, populations of plants with long peduncles.)

TYPE: Cuba, Santa Clara, Sabana de Montembo, *León & Loustalot 11343* (holotype, Colegio de la Salle, Vedado, Havana, not seen; isotype, GH!).

Andropogon elliottii Chapman var. *projectus* Fern. & Griscom, Rhodora **37:** 138, 139. 1935. TYPE: North Carolina, Buncombe County, *Baltimore 1421*ᶜ, 1898 (holotype, GH!; isotypes, NCU!, NY!, US (two sheets)!).

DIAGNOSIS. Ligules short.

DISTRIBUTION. Same as the species.

2a. 1. **Common variant** FIGURES 11, A, B; 29; 30.

DIAGNOSIS. Raceme sheaths hidden within overlapping and more or less inflated upper stem sheaths.

DISTRIBUTION. Generally dry, sandy soil of roadsides, embankments, fields, pine or oak woods; occasionally in moister soil. New Jersey to Missouri, south to Florida and Texas; Mexico (Beetle, 1977); Belize; Honduras; Cuba (MAP 9).

REPRESENTATIVE SPECIMENS. **United States.** NEW JERSEY: Atlantic, *Long 14026* (GH); Camden, *Long 15430* (GH); Cape May, *Mackenzie 6695* (DUKE, MICH, MO, NY); Cumberland, *Long 29696* (GH); Gloucester, *Lippincott s.n.*, 1894 (GH); Salem, *Long s.n.*, 1909 (GH, NY). PENNSYLVANIA: Bucks, *Long 65639* (GH); Chester, *Pennell 8889* (NY); Delaware, *Bartram 1383* (GH); Montgomery, *Fogg 5384* (GH); Philadelphia, *Crosby s.n.*, 1942 (GH). DELAWARE: New Castle, *Long 57766* (GH); Sussex, *Churchill s.n., s.d.* (MO). MARYLAND: Baltimore, *Taylor s.n.*, 1890 (MICH); Caroline, *Wilkens 5057-a* (NCU); Cecil, *Tatnall 4411* (GH); Montgomery, *Hitchcock 251* (GH, MO, NY, US); Prince George's, *Blake 9733* (GH); Queen Anne's, *Commons s.n.*, 1870 (NY). DISTRICT OF COLUMBIA: *Steele s.n.*, 1896 (DUKE, GH, NY). WEST VIRGINIA: Cabell, *Millender s.n.*, 1939 (NY); Jackson, *Richardson s.n.*, 1955 (NCU). VIRGINIA: Arlington, *Allard 91a* (DUKE, GH, MO, NY); Bedford, *A. H. Curtiss 9868* (MO); Brunswick, *Fernald & Lewis 14475* (GH); Culpepper, *Ahles & James 61644* (NCU); Dinwiddie, *Swallen 5527* (US); Fairfax, *Fosberg 30198* (GH); Fauquier, *Allard 3891* (GH); Greensville, *Fernald & Long 9250* (GH); Lunenburg, *Ahles & James 61944* (NCU); Nansemond, *Fernald & Long 6761* (GH, MO, NY); Norfolk, *Kearney 2383* (US); Northampton, *Fernald et al. 5786* (GH); Prince Edward, *Ahles & James 62685* (NCU); Prince William, *Hermann 9911* (GH, MO, NY). NORTH CAROLINA: Anson, *Correll 7091* (DUKE, GA, MICH); Beaufort, *Ashe* (NCU); Bertie, *Ahles & Haesloop 52163* (NCU); Buncombe, *Biltmore 1421*ᵇ (GH, NCU, NY, US); Granville, *Dayton 1715* (NCU); Harnett, *Boyce et al. 1608* (NY, US); Gates, *Godfrey 7039* (DUKE, GH); Forsyth, *Ahles & Haesloop 51646* (NCU); Durham, *Godfrey 6729* (GH); Davidson, *Denke s.n.*, 1826 (DUKE); Cumberland, *Ahles 36592* (FSU, NCU); Craven, *Blomquist 11423* (DUKE); Brunswick, *Blomquist 413* (GH); Bladen, *Ahles 37423* (NCU, USF); Hertford, *Ahles & Haesloop 52209* (NCU); Hyde, *Radford 42668* (NCU); Lee, *Correll 6977* (DUKE, GH); Lenoir, *Radford 31634* (NCU); Mecklenberg, *Batson 408* (DUKE); Moore, *Correll 7214* (DUKE); Nash, *Godfrey & Kerr 6644* (DUKE, GH); Northampton, *Ahles 52459* (NCU); Orange, *Blomquist 466* (DUKE); Pamlico, *Radford 42295* (NCU); Pender, *Ashe 319* (NCU); Person, *Bowmer 147* (NCU); Richmond, *Correll 7134* (DUKE, GH); Sampson, *Campbell 3994* (GH); Scotland, *Godfrey 6946* (GH); Stokes, *Ashe s.n.*, 1896 (NCU); Transylvania, *Cain 265* (TENN); Wake, *Blomquist 119* (US); Wayne, *Radford 31497* (NCU); Vance, *Ahles & Leisner 20288* (NCU). SOUTH CAROLINA: Aiken, *Ahles & Crutchfield 55181* (NCU); Allendale, *Bell 5124* (NCU, US); Bamberg, *Campbell 4008* (GH); Barnwell, *Batson & Kelley s.n.*, 1959 (NCU); Calhoun, *Ahles 35306* (GA, NCU); Charleston, *Ahles & Haesloop 38652* (NCU); Dillon, *Ahles 37103* (GH, NCU); Dorchester, *Ahles & Haesloop 37859* (NCU); Florence, *Campbell 3967* (GH); Hampton, *Ahles & Bell 20922* (NCU); Kershaw, *Radford 30043* (NCU, NY); Lexington, *Radford 29877* (NCU, VDB); Orangeburg, *Ahles 35136* (NCU); York, *Ahles 34490* (NCU).

GEORGIA: Baker, *Godfrey 67566* (FSU, US); Bartow, *Duncan et al. 12110* (GA); Berrien, *Celarier A-2588-1* (MO); Brantley, *Campbell 4026* (GH); Butts, *Campbell 4143* (GH); Calhoun, *Thorne 6863* (GA); Charlton, *Campbell 4139* (GH); Clarke, *Miller s.n.*, 1941 (US); Decatur, *Godfrey 74097* (FSU, NCU); Dougherty, *Eyles 7666* (DUKE); Lincoln, *Pyson & McVaugh 92* (GA); McIntosh, *Bozeman & Ahles 2476* (NCU); Oglethorpe, *Harper 656* (DUKE, GA); Screven, *Eyles 7569* (DUKE); Tift, *Celarier A-2608-1* (MO); Toombs, *Duncan & Hardin 14522* (NCU); Thomas, *Campbell 4180* (GH). FLORIDA: Alachua, *Swallen 5626* (US); Bay, *Godfrey 61605* (FSU); Brevard, *Fredholm 6134* (GH, US); Calhoun, *Godfrey 61601* (DUKE, FSU, US, USF, VDB); Clay, *Campbell & Godfrey 4139* (GH); Collier, *Deam 65368* (US); Columbia, *DeSelm s.n.*, 1969 (TENN); Dade, *Eaton s.n.*, 1903 (GH, US, VT); Duval, *A. H. Curtiss 3636a* (FSU, GH, MICH, MISSA, MO, NCU, US); Franklin, *Campbell 3932* (GH); Gadsden, *Godfrey 64939* (FSU, VDB); Gilchrist, *Godfrey 65098* (FSU); Gulf, *Silveus 6732-A* (GA, TAES); Highlands, *Brass 15647* (GH, US); Hillsborough, *Lakela 23700* (FSU, US, USF); Jackson, *Campbell 3782* (GH); Jefferson, *Campbell 4069* (GH); Lake, *Silveus 6689* (TAES); Lee, *Kellogg 27041* (MO); Leon, *Kral 1805* (DUKE, FSU, NY); Levy, *Campbell 4095* (GH); Liberty, *Godfrey 73140* (FSU); Madison, *Kral 6188* (DUKE, FSU, GH, VDB); Martin, *Campbell 3872* (GH); Okaloosa, *Godfrey 76203* (FSU); Pinellas, *Tracy 7768* (GH, MO, NY, WIS); Polk, *Lakela 23588* (USF, VDB); Putnam, *Godfrey & Morrill 52629a* (DUKE, FSU); Orange, *Baker 63* (US); Osceola, *Fredholm 6098* (GH); Suwannee, *DeSelm s.n.*, 1969 (TENN); Wakulla, *Godfrey & Morar 61587* (DUKE, FSU, US); Walton, *Godfrey 55250a* (FSU, GH, NCU, USF). OHIO: Highland, *Braun s.n.*, 1961 (US); Jackson, *Bartley & Pontius 814* (NY, US); Jefferson, *Jones s.n.*, 1935 (NY); Pike, *Bartley 2989* (NY); Vinton, *Musgrove 770* (NCU). INDIANA: Clark, *Seaver 26865* (GH, US); Floyd, *Deam 51650* (US); Lawrence, *Kriebel 1441* (DUKE); Orange, *Deam 33395½* (US); Perry, *Deam 39976* (US); Vanderburgh, *Deam 33104* (US). KENTUCKY: Barren, *Braun 3636* (US); Christian, *Labisky 279* (WIS); Edmonson, *Braun 3563* (US); Fleming, *Braun 1743* (GH, US); Lyon, *Athey 3877* (FSU); McCreary, *Braun 482* (US); Meade, *Sargent 100* (GH); Wayne, *Braun 2834* (US). TENNESSEE: Blount, *Thomas s.n.*, 1964 (TENN); Coffee, *Gattinger s.n.*, 1880 (MICH); Cumberland, *Jennison 3394* (TENN); Davidson, *Gattinger s.n., s.d.* (NY); Fentress, *Rogers 41376* (TENN); Hickman, *Kral 4357* (VDB); Knox, *Ruth s.n.*, 1894 (NY); McNairy, *Shanks et al. 14704* (TENN); Montgomery, *Shanks 1077* (TENN); Morgan, *Rogers 41376* (NCU); Roane, *Rogers 41402* (NCU, TENN, VDB); Stewart, *Ellis & Clebsch 930* (NCU); Van Buren, *Iltis 3405* (TENN); White, *DeSelm 218* (TENN). ALABAMA: Baldwin, *Kral 29768* (VDB); Barbour, *Kral 38017* (VDB); Bibb, *Campbell 3959* (GH); Coffee, *Kral 41685* (VDB); Covington, *Kral 33656* (TENN, VDB); Cullman, *Eggert s.n.*, 1898 (MO); Crenshaw, *Kral 41605* (VDB); Lauderdale, *Kral 29353* (GA, VDB); Lee, *Earle & Baker s.n.*, 1897 (MICH, MO, NCU, NY); Marengo, *Kral 29588B* (FSU, VDB); Mobile, *Mohr s.n.*, 1889 (NY); St. Clair, *Kral 37930* (VDB); Washington, *McDaniel 9915* (GA, VDB). MISSISSIPPI: Amite, *Ray 5471* (MISSA); Forest, *Rogers 7045* (NCU, TENN); Harrison, *Tracy 8394* (GH, MO, NY, US, WIS); Lafayette, *Burke 66* (MISS); Lamar, *Jones 2951* (GA); Marshall, *Lasseter 589* (MISS); Pearl River, *Reed 34* (FSU, VDB); Wayne, *Kearney 163* (US). ILLINOIS: Hardin, *Evers 21903* (MO, WIS); Saline, *Evers 67370* (NCU, WIS). MISSOURI: Barry, *Mackenzie s.n.*, 1896 (NY); Franklin, *Shea 299* (MO); Jefferson, *Eggert s.n.*, 1886 (GH); Phelps, *Steyermark 20905* (MO); Shannon, *Steyermark 16339* (GH, MO); St. Genevieve, *Steyermark 8290* (GH, MO); Washington, *Steyermark 77858* (US). ARKANSAS: Ashley, *Iltis 25312* (WIS); Conway, *Moore 321046* (WIS); Izard, *Robinson 2134A* (GH, NY, US); Lawrence, *Robinson 2223* (NY); Pope, *Lawson s.n.*, 1949 (NCU); Pulaski, *Engelmann 78* (MO); Searcy, *Robinson 2184* (US); Stone, *Hatcher s.n.*, 1951 (NCU). LOUISIANA: Beauregard, *Heyne 1381* (US); Grant, *Ewen 17506* (MO); LaSalle, *Swallen 10501* (US); Lincoln, *Kral 16119* (FSU, VDB); Rapides, *Cassady s.n.*, 1952 (TAES); Sabine, *Kral 16219* (FSU, VDB). OKLAHOMA: Le Flore, *Waterfall 9848* (US). TEXAS: BRAZOS, *Sperry 2566* (TAES); Erath, *Hancock 64-8* (TAES); Galveston, *Waller & Bauml 3208A* (GH, TAES); Robertson, *Lincecum 31* (TAES); Walker, *McCleod s.n.*, 1957 (TAES). **Belize.** El Cayo Distr., San Augustin, *Lundell 6727* (MICH, NY). **Honduras.** El Paraíso, *Standley 29035* (F). **Cuba.** LAS VILLAS: Santa Clara, Sabana de Motembo, *León 11343* (GH).

I include three previously described varieties in the common variant, so called because of its high frequency of occurrence in nature. Scribner distinguished his *Andropogon elliottii* var. *laxiflorus* from *A. elliottii* Chapman var. *elliottii* on the basis of the upper stem sheaths of the former not being inflated and overlapping. In addition, he noted the long rachis internodes ("joints") of his variety. In Florida, Mississippi, Louisiana, and South Carolina there are at least eight populations that resemble Scribner's type in having all the internodes of the upper part of the stem elongate. While these elongations make the plants quite distinctive, they appear to represent merely an abnormality of plants of the common variant of *A. gyrans* var. *gyrans*. One of the specimens (*Nash 1759* (NY!)) cited by Nash in his protologue of *A. campyloracheus* (based on *A. elliottii* var. *laxiflorus*) as being from the type locality has two stems that are connected at the base. One of these has the elongate internodes of Scribner's *A. elliottii* var. *laxiflorus*, and the other has the overlapping, inflated upper stem sheaths characteristic of the common variant of *A. gyrans* var. *gyrans*. The cause of this possible abnormality is unknown, but two observations may be of importance. First, all these abnormal plants flower earlier than is normal for the common variant. Second, half of the populations contain some plants that are viviparous, the flowers being replaced by small plantlets. It is not known whether or not these plantlets are effective in reproducing the parent plant. Their frequency of occurrence in nature in the virginicus complex as a whole is extremely low.

Fernald and Griscom named *Andropogon elliottii* var. *projectus* without appreciating the variability of peduncle length, the single distinguishing character of this variety. There is more or less continuous variation between plants with short peduncles and entirely hidden (and cleistogamous-flowered) racemes, and plants with some racemes hidden and some exposed on long peduncles. Very infrequently, some plants may have all or many of the racemes exserted above the apex of the raceme sheaths. Moreover, the claim that this taxon has a "notable geographic segregation" (Fernald & Griscom, 1935) is unsupportable since there does not appear to be any geographic pattern to variation in peduncle length.

Andropogon elliottii var. *gracilior* was based solely on overall plant size. I have seen populations of noticeably smaller individuals. They do not seem to be juvenile since their size remained consistent over the two years during which I observed them. Their size is apparently not a phenotypic response to poor soil conditions since I have seen short and tall plants within 50 m of one another in a uniform flatwoods locality in southern Florida. Regardless of these observations, plant size is far too variable in the common variant to warrant recognition of this variety.

2a. 2. **Tenuous variant** FIGURES 11, E, F; 31.

DIAGNOSIS. Raceme sheaths visible after anthesis.

DISTRIBUTION. Sandy, moist or dry soil. Florida and Mississippi (MAP 10).

REPRESENTATIVE SPECIMENS. **United States.** FLORIDA: Brevard, *Campbell 3765* (GH); Charlotte, *Hitchcock 440* (GH); Collier, *Lakela 31196* (GH); Franklin, *Godfrey 75579* (FSU);

Highlands, *Campbell 3746* (GH); Hillsborough, *Lakela 25249* (GH); Lee, *Hitchcock 440* (GH, MO, NY, US); Manatee, *Perdue 1789* (FSU, GH, NCU, TAES, USF); Martin, *Campbell 3873* (GH); Pinellas, *Lakela 27621* (USF); Volusia, *Shuey & Poppleton 1544* (USF). MISSISSIPPI: Harrison, *Tracy 4701* (GH, TAES, US); Jackson, *Tracy 2243* (NY).

This taxon includes two kinds of plants. One has both long- and short-peduncled racemes—and hence both chasmogamous and cleistogamous flowers—on the same stem. I have seen this kind only once (Florida, Martin Co., *Campbell 3873*) in the field. There are two other populations in southern Mississippi (MAP 10), one of which is the source of the lectotype of *Andropogon subtenuis* Nash (*Tracy 2243* (NY); Hitchcock, 1951). The second kind has only short peduncles and predominantly cleistogamous flowers. It has neither been described formally nor discussed in any previous publications concerning the virginicus complex. Invariably it has been identified as *A. virginicus.*

As its name implies, the tenuous variant is difficult to circumscribe. It differs from the common variant quite strikingly in the one character provided in their diagnoses. Nevertheless, there are plants of intermediate morphology that are not readily placed into either taxon. The best way to distinguish the tenuous variant from *Andropogon gyrans* var. *stenophyllus* is by comparing the ligules; the latter taxon also occurs more frequently and ranges farther in more poorly drained soils.

2b. **Andropogon gyrans** Ashe var. **stenophyllus** (Hackel) Campbell, comb. nov. FIGURES 11, C, D; 32; 33.

BASIONYM: *Andropogon virginicus* L. subvar. *stenophyllus* Hackel in DC. Monogr. Phanerog. **6:** 411. 1889. TYPE:[3] Florida, *Chapman s.n., s.d.* (lectotype, W!; isolectotype, W!). *Andropogon virginicus* L. var. *stenophyllus* (Hackel) Fern. & Griscom, Rhodora **37:** 142. 1935.

Andropogon perangustatus Nash in Small, Fl. SE. U. S. 62. 1903. Based on *Andropogon virginicus* L. subvar. *stenophyllus* Hackel. Not *Andropogon stenophyllus* Roemer & Schultes, 1817.

DIAGNOSIS. Ligules long, with marginal ciliations short.

DISTRIBUTION. Ditches, bogs, savannas, and pond margins. Coastal Plain from North Carolina to eastern Texas (MAP 11).

REPRESENTATIVE SPECIMENS. **United States.** NORTH CAROLINA: Robeson, *Ahles 37246* (NCU); Wilson, *Radford 40687* (NCU). SOUTH CAROLINA: Saluda, *Radford 30369* (NCU). GEORGIA: Berrien, *Harper 1707* (GH, MO); Charlton, *Campbell 4138* (GH); Colquitt, *Godfrey 76086* (FLAS); Emanuel, *Plummer & Pullen 1962* (GA); Thomas, *Campbell 41481* (GH). FLORIDA: Brevard, *Fredholm 6193* (US); Clay, *Campbell 4137* (GH); Duval, *A. H. Curtiss 6016* (FSU, GA, GH, MO, NCU, NY, TAES, US, VT); Franklin, *Campbell 3822* (GH); Gulf, *Chapman s.n.* (GH, MO); Highlands, *Swallen 5368*; Hillsborough, *Fredholm 6427* (GH); Indian River, *Tracy 9298* (TAES, US); Jackson, *Campbell 3813* (GH); Jefferson, *Campbell 4070* (GH); Liberty, *Campbell 3829* (GH); Osceola, *Fredholm 6072* (US); Pasco, *Ray 9594* (US, USF); Putnam, *Godfrey 76892* (FSU); St. Lucie, *Silveus 6664* (TAES); Volusia, *Silveus 6529* (DUKE, GA, TAES); Wakulla, *Lamp 17* (FSU); Walton, *A. H. Curtiss 6928*

[3]Hackel cited "Florida (Chapman) et Alabama (Mohr)." There are two Chapman sheets of a Florida collection and one Mohr collection (Alabama, Mobile County, *s.n.*) in the Hackel herbarium at W. One of the Chapman specimens is here designated the lectotype.

(GA, GH, MO, NY, US). ALABAMA: Baldwin, *Kral 38228* (GH, US, VDB); Geneva, *Kral 52006* (VDB). MISSISSIPPI: Harrison, *Tracy 3830* (MICH, MO, NY); Jackson, *Earle 1890* (TAES); Pearl River, *Reed 40* (FSU). LOUISIANA: East Baton Rouge, *Brown 1499* (US); Grant, *McKellar 272* (US); Rapides, *Duncan 1956* (TAES). TEXAS: Galveston, *Waller & Bauml 3325* (GH, TAES); Robertson, *Hatch 2108* (TAES).

Like the tenuous variant of *Andropogon gyrans* var. *gyrans, A. gyrans* var. *stenophyllus* consists of two kinds of plants differing in flowering mode. The short-peduncled, cleistogamously flowering plants tend to grow in relatively disturbed sites such as roadside ditches and have a much wider range than the mostly long-peduncled and often chasmogamous plants. I have seen only three populations of the latter kind, all in infrequently disturbed boggy sites. Two of the populations contained predominantly chasmogamous-flowered plants. In the third locality, a rather wet flatwoods in Franklin County, Florida, was a mixture of the two flowering modes (*Campbell 3822*), with the chasmogamous type predominating. The two types of plants differ in three ways (see TABLE 7), which hold for nonmixed populations of both kinds of plants. It is not known whether or not these two kinds are genetic segregates of one another. They are not separated as taxa because they do not differ morphologically in any ways other than the three usually correlated characters, and these characters vary within a single population.

3. **Andropogon tracyi** Nash, Bull. New York Bot. Gard. **1:** 433. 1900. TYPE: Mississippi, Lowndes County, *Tracy 3083,* 1895 (holotype, NY!).
FIGURES 11, T; 35.

DIAGNOSIS. Stems short; leaves narrow; inflorescence units few per stem; peduncles, spikelets, and anthers long.

DISTRIBUTION. Sandhills, sandy pinelands and scrublands. Coastal Plain from North Carolina to Mississippi (MAP 8).

REPRESENTATIVE SPECIMENS. **United States.** NORTH CAROLINA: Gates, *Ahles & Duke 51584* (NCU); Granville, *Dayton 1267* (NCU); Harnett, *Radford 8762* (NCU); Johnston, *Radford 29156* (NCU); Pender, *Wells s.n.,* 1925 (NY); Sampson, *Campbell 3993* (GH); Scotland, *Ahles 36966* (NCU). SOUTH CAROLINA: Aiken, *Miller s.n.,* 1966 (NCU); Allendale, *Campbell 3716* (GH); Bamberg, *Campbell 4007* (GH); Beaufort, *Cuthbert s.n.,* 1902 (FLAS); Charleston, *Ahles & Haesloop 38051* (NCU). GEORGIA: Chatham, *Eyles 6645* (US); Screven, *Campbell 4203* (GA); Talbot, *Jones s.n.,* 1959 (GA); Toombs, *Hardin & Duncan 14526* (GA). FLORIDA: Bay, *Kral 52173* (VDB); Dade, *Small et al. 897* (NY); Calhoun, *Grelen 11/58-7* (FSU); Duval, *A. H. Curtiss 4012a* (NY); Highlands, *Davis s.n.,* 1941 (FLAS); Hillsborough, *Fredholm 6423* (US); Orange, *Baker 329* (S); Putnam, *Campbell 4100* (GH); Walton, *McDaniel 7145* (FSU, VDB). ALABAMA: Baldwin, *Kral 29797* (US, VDB); Clarke, *Kral 29570B* (VDB); Henry, *Kral 48974* (VDB); Lee, *Earle & Baker 1456* (MO, NY, US); Mobile, *Langlois s.n.,* 1880 (MO); Pike, *Kral 52222* (VDB). MISSISSIPPI: Forrest, *Rogers 7047* (NCU, VDB); Harrison, *Earle s.n.,* 1899 (NY); Jasper, *McDaniel 2796* (MO, NY); Lowndes, *Tracy s.n.,* 1895 (US); Pearl River, *Sargent 8668* (VDB).

Earlier workers have noted a similarity between *Andropogon tracyi* and *A. longiberbis,* and the two species are indeed similar in general aspect. They differ, however, in overall size, in amount and orientation of leaf pubescence, and in length of the peduncle, spikelet, and anther. *Andropogon tracyi* also has

TABLE 7. **Comparison of the morphology of two kinds of plants* of Andropogon gyrans var. stenophyllus.**

MEAN (± S.E.) PERCENT CHASMOGAMY	SAMPLE SIZE	PEDUNCLE LENGTH (mm)	SPIKELET LENGTH (mm)	ANTHER LENGTH (mm)
73 (8)†	9	(8–)12–22(–45)	(4.4–)4.7–5.2(–5.5)	(1.1–)1.4–1.5(–1.7)
30 (6)	4	(4.5–)5–5.5(–6)	(4–)4.2–4.5(–5.2)	(0.9–)1–1.2(–1.3)

*Both kinds from *Campbell 3822*, Franklin County, Florida.
†For the meaning of the measurements in this table, see explanation in Character States section.

a wider, more northerly range. It is possible that a shift in flowering mode toward cleistogamy in the ancestral stock of *A. tracyi* may have given rise to ancestors of *A. longiberbis*. However, in the other instances in the complex where such a change in flowering mode can be inferred, there is a pronounced similarity in other specialized characters that strongly tie the taxa to one another. No such specialized characters in *A. tracyi* and *A. longiberbis* suggest a common ancestry.

The resemblance of *Andropogon tracyi* and *A. gyrans*, particularly the tenuous variant of var. *gyrans*, is also great. The tenuous variant has peduncles that are either variable or all short on an individual plant, smaller spikelets, and shorter anthers.

4. **Andropogon liebmannii** Hackel, Flora **68:** 132. 1885. TYPE:[4] Mexico, Chinantla, *Liebmann 77* (lectotype, C!; isolectotypes, C!, GH (two sheets)!, MICH!, UC (two sheets)!, US (three sheets)!). *Sorghum liebmannii* (Hackel) Kuntze, Rev. Gen. Pl. **2:** 792. 1891. *Anatherum virginicum* (L.) Sprengel subvar. *liebmannii* (Hackel) G. Roberty, Boissiera **9:** 213. 1960.

DIAGNOSIS. Peduncles all long, usually bearing 4 or more racemes; raceme sheaths long; spikelets broad.

DISTRIBUTION. Generally moist ground. Mexico and Coastal Plain of southeastern United States.

The two varieties of *Andropogon liebmannii* have been treated as distinct species by most American authors. However, the morphological distance of 9 separating them (TABLE 6) is based primarily on differences of size, which possibly arise either from dissimilar growing conditions in Mexico and the

[4]Although Hackel cited *Liebmann 590* from Chinantla, Mexico, A. F. Maule of the Botanical Museum in Copenhagen notes (pers. comm.) that Liebmann's numbers were not collector's numbers but a systematic arrangement after his return; no. *590* was at Berlin and destroyed(?). Several other Liebmann specimens from Chinantla (none of them from W) bear Hackel's determination. One of these has been chosen as the lectotype. Hackel also cited *Bourgeau 2376*, but the only specimen of this collection that I have examined (Mexico, Veracruz, 1865–1866 (GH!)) bears no indication that Hackel saw it.

southeastern United States or from pleiotropy of one or more genes controlling size. The two varieties share a character state (raceme number—character 22 of TABLE 4) found only in these two taxa, and they are strongly similar in most qualitative characters, flowering mode, and preference for wet soils.

4a. **Andropogon liebmannii** Hackel var. **liebmannii** FIGURE 36.

Andropogon liebmannii Hackel subvar. *raripilus* Hackel in DC. Monogr. Phanerog. **6:** 413. 1889. TYPE: Mexico, Jalisco, *Palmer 227,* 1886 (holotype, not seen; isotypes, GH!, UC!, VT!).

DIAGNOSIS. Small (in stem height, leaf-blade length, maximum inflorescence branching and sympodia, and inflorescence units per stem); leaves often only sparsely pubescent.

DISTRIBUTION. Swales, banks, fields, and pinelands to 2200 m alt. Central volcanic belt of Mexico (MAP 7).

REPRESENTATIVE SPECIMENS. **Mexico.** NAYARIT: Tepic, *Rose 2222* (GH), *McVaugh et al. 16434* (MICH). JALISCO: Los Colomos, *Villarreal de Puga 4061* (MICH); near Guadalajara, *Palmer 227* (GH, UC, VT), *Pringle 11212* (F, GH, VT). MICHOACÁN: near Ciudad Hidalgo, *Gould 9613* (UC), *Kral 25539* (VDB); Uruapan, *Hitchcock 263* (F, GH, UC). MÉXICO: Temascaltepec, *Hinton 1413* (GH). PUEBLA: Chinantla, *Liebmann s.n.,* 1841 (C, GH, MICH, UC). HIDALGO: Agua Blanca, *Moore 2064* (GH). VERACRUZ: Tzuatlanchillo, *Bourgeau 2376* (GH).

Andropogon liebmannii var. *liebmannii* flowers during August and September, and infrequently in May and June. It is either a rather rare or an under-collected taxon presently known from only 12 localities.

4b. **Andropogon liebmannii** var. **pungensis** (Ashe) Campbell, comb. nov. FIGURES 11, J; 37; 38.

BASIONYM: *Andropogon mohrii* (Hackel) Vasey var. *pungensis* Ashe, Jour. Elisha Mitchell Sci. Soc. **15:** 113. 1899. TYPE: North Carolina, Washington County, *Ashe 1898* (holotype, NCU!).

Andropogon liebmannii Hackel subvar. *mohrii* Hackel in DC. Monogr. Phanerog. **6:** 413. 1889. TYPE: Alabama, Mobile County, *Mohr s.n.,* 1888 (holotype, US!). *Andropogon mohrii* (Hackel) Vasey, Contr. U. S. Natl. Herb. **3:** 11. 1892. *Anatherum virginicum* (L.) subvar. *mohrii* (Hackel) G. Roberty, Boissiera **9:** 213. 1960.

DIAGNOSIS. Large (relative to var. *liebmannii* in characters listed in diagnosis of that taxon); leaves usually densely pubescent.

DISTRIBUTION. Bogs, swamps, savannas, and flatwoods. Coastal Plain from Virginia to Louisiana; relatively infrequent in Florida (MAP 6).

REPRESENTATIVE SPECIMENS. **United States.** VIRGINIA: Dinwiddie, *Swallen 5541* (US); Prince George, *Fernald et al. 6758* (GH). NORTH CAROLINA: Pender, *Blomquist 10064* (DUKE, GH, NY, US); Robeson, *Ahles 37317* (NCU); Washington, *Ashe s.n.,* 1898 (NCU). GEORGIA: Bullock, *Plummer & Pullen s.n.,* 1962 (GA); Irwin, *Harper 1708* (GH, MO, NY); Tift, *Plummer & Pullen s.n.,* 1962 (GA); Wheeler, *Plummer & Pullen s.n.,* 1962 (GA). FLORIDA: Escambia, *Campbell 3948* (GH); Franklin, *Godfrey 79254* (FSU); Jackson, *Campbell 3913* (GH); Liberty, *Godfrey 78259* (FSU); Washington, *Godfrey 80130* (FSU).

FIGURES 36–41. 36, *Andropogon liebmannii* var. *liebmannii* (*Kral 25539*, Mexico), portion of inflorescence. 37, 38, *A. liebmannii* var. *pungensis* (*Campbell 3948*): 37, portion of inflorescence; 38, stem. 39, 40, *A. floridanus* (*Campbell 4194*): 39, basal clump of leaves; 40, inflorescences at different stages (left, mature fruit; middle, young fruit; right, anthesis). 41, *A. longiberbis* (*Campbell 4098*), two inflorescences. Scale = 15 cm.

ALABAMA: Baldwin, *Tracy 8604* (GH, MO, TAES, US); Butler, *Kral 41632* (VDB); Escambia, *Kral 44845* (VDB); Mobile, *Mohr s.n., s.d.* (MISSA, NCU, NY, TAES, US); Washington, *Kral 29542* (NCU, VDB). MISSISSIPPI: Hancock, *Rogers 2498* (NCU, TENN, VDB); Harrison, *Tracy 3895* (DUKE, GH, NCU, NY, US, W); Jackson, *Demaree 34499* (GA, MISSA, TAES, US, VDB); Pearl River, *Sargent 9027* (GA, MISS); Stone, *DeSelm 1969* (TENN). LOUISIANA: Orleans, *Drummond s.n.*, 1832 (NY); Calcasieu, *Drummond s.n.*, 1833 (US).

Andropogon liebmannii var. *pungensis* forms small, infrequent populations in little-disturbed boggy sites. The often densely pubescent stem sheaths, the number of racemes per inflorescence unit, and the large spikelets make this variety easily identifiable. Some botanists have confused it with the old-field variant of *A. virginicus* var. *virginicus* (e.g., Kral's (1976) report of this taxon from Franklin County, Florida, is based on *Kral 52387*, which is actually the old-field variant of *A. virginicus* var. *virginicus*). These two taxa are similar in their densely pubescent stem sheaths and numerous racemes per inflorescence unit. They are best distinguished by peduncle length and spikelet dimensions.

5. **Andropogon floridanus** Scribner, Bull. Torrey Bot. Club **23:** 145. 1896. TYPE: Florida, Lake County, *Nash 1572*, 1894 (holotype, US!; isotypes, GH!, US (two sheets)!). *Anatherum virginicum* (L.) Sprengel subvar. *floridanum* (Scribner) G. Roberty, Boissiera **9:** 212. 1960.

FIGURES 11, H; 39; 40.

Andropogon bakeri Scribner & Ball, Bull. U. S. D. A. Div. Agrost. **24:** 39. 1901. TYPE: Florida, Orange County, *Baker 58*, 1897 (holotype, US, not seen; isotypes, GH!).

DIAGNOSIS. Leaves long, glabrous; peduncles long; hairs of rachis internode uniformly distributed, not becoming sparse toward base.

DISTRIBUTION. Sandy soils in southeastern Georgia and Florida; in *Pinus clausa* (Chapman) Vasey scrublands in eastern Florida (MAP 4).

REPRESENTATIVE SPECIMENS. **United States.** GEORGIA: Long, *Bozeman 1979* (GA, NCU). FLORIDA: Alachua, *Gould 6671* (TAES); Brevard, *Fredholm 6008* (GH, MO, US); Citrus, *Combs 976* (GH, US); Collier, *Lakela 31191* (GH, USF); Franklin, *Silveus 6503* (TAES, US); Hernando, *Ray 9530* (GH, NCU, US, VDB); Highlands, *Campbell 3887* (GH); Hillsborough, *Garber 1877* (GH, VT, W); Lake, *Nash 1681* (GH, NY, US); Lee, *Chase 4176* (US); Leon, *Kral 1801* (DUKE); Levy, *Cooley et al. 7174* (NCU, USF, WIS); Manatee, *Combs 1291* (US); Marion, *Campbell 4194* (GH); Martin, *Campbell 3754* (GH); Orange, *Campbell 3860* (GH); Osceola, *Fredholm 6072* (GH); Palm Beach, *Hitchcock 2264* (US); Polk, *Lakela 24273* (GH, NCU, USF); Putnam, *Laessle s.n.*, 1960 (US); St. John, *Silveus 6744* (US); St. Lucie, *Silveus 5294* (TAES); Sarasota, *Kral 51971* (VDB); Seminole, *Beardslee 41* (US); Volusia, *Hood 32* (US).

Plants of this species are easily distinguished from the rest of the virginicus complex by morphology and ecological preferences. The uniform distribution of pubescence on the rachis internodes is a unique and constant character. Laessle (1958) found *Andropogon floridanus* to be a good indicator of *Pinus clausa* scrub vegetation, an association confined to Florida. Other broomsedges may sometimes grow with *P. clausa*, but they characteristically invade more disturbed sites. *Andropogon floridanus* usually occurs in small populations of scattered individuals, but several stands of hundreds of individuals have been observed in clear-cut scrub pine (*P. clausa*) timberlands in central Florida.

6. **Andropogon longiberbis** Hackel, Flora **68:** 131, 132. 1885. TYPE:[5] Florida, *Garber 1877* (lectotype, W!; isolectotypes, MO!, NY!, US!, W (two sheets)!). *Sorghum longiberbe* (Hackel) Kuntze, Rev. Gen. Pl. **2:** 792. 1891. *Anatherum virginicum* (L.) subvar. *longiberbe* (Hackel) G. Roberty, Boissiera **9:** 213. 1960. FIGURES 11, I, J; 41.

DIAGNOSIS. Leaf pubescence mostly appressed; raceme sheaths rather broad; spikelets long; callus hairs long.

DISTRIBUTION. Sandy or rocky soils of roadsides, dunes, sandhills, pinelands, and fields. Southern South Carolina to Florida and Bahamas (MAP 2); common only in Florida.

REPRESENTATIVE SPECIMENS. **United States.** NORTH CAROLINA: New Hanover, *Schallert 1935* (DUKE). SOUTH CAROLINA: Beaufort, *Bell 1956* (NCU). GEORGIA: McIntosh, *Duncan 20605* (DUKE, FLAS, MISS, TENN, WIS). FLORIDA: Alachua, *Campbell 3854* (GH); Brevard, *Campbell 3764* (GH), *Small et al. 3352* (NY); Charlotte, *Parrott 81* (DUKE); Clay, *Campbell 4134* (GH); Collier, *Deam 60590* (DUKE); Columbia, *Godfrey 76903* (FSU); Dade, *Campbell 3729* (GH); Duval, *A. H. Curtiss 5571* (GA, GH, MO, NCU, NY); Flagler, *Young s.n.*, 1940 (GA); Franklin, *Godfrey 77349* (FSU); Gilchrist, *Campbell 3910* (GH); Hernando, *Correll 5845* (GH, US); Hillsborough, *Lakela 24138* (FSU, GH, NCU); Jackson, *Campbell 4032* (GH); Lake, *Nash 645* (GH, NY, TAES, US); Lee, *Standley 169* (GH, NY, US); Leon, *Kral 1837* (GH); Levy, *Campbell 4097* (GH); Madison, *Godfrey 75784* (FSU); Manatee, *Rugel 232* (NY, US, USF); Marion, *Campbell 4108* (GH); Monroe, *Campbell 4225* (GH); Nassau, *Godfrey 74687* (FLAS); Okeechobee, *Silveus 5776* (US); Orange, *Baker 49* (GH, NY); Osceola, *DeSelm 1969* (TENN); Pinellas, *Tracy 7185* (GH, NY, TAES, US, W, WIS); Polk, *Cooley et al. 8251* (GH, USF); Putnam, *Campbell 4089* (GH); Seminole, *Schallert 20854* (WIS); Suwannee, *Campbell 3847* (GH); Taylor, *Godfrey 75778* (FSU); Volusia, *Hood 41* (US); Wakulla, *Campbell 4063* (GH). **Bahama Islands:** Grand Bahama, *Correll & Kral 43036* (VDB).

Andropogon longiberbis is related to several other members of the virginicus complex. It apparently hybridizes with both the old-field variant of *A. virginicus* var. *virginicus* and the robust variant of *A. glomeratus* var. *pumilus* (see section on hybridization), suggesting some affinities. The morphological gap of 6.5 between *A. longiberbis* and *A. virginicus* is the smallest of all interspecific gaps. Furthermore, the gaps between *A. longiberbis* and two of the three variants of var. *virginicus* are only 7 and 6.5. However, there are three morphological differences that always hold: leaf-pubescence orientation, callus-hair length, and spikelet length. These differences and the abundance of *A. longiberbis* in southernmost Florida (where *A. virginicus* is quite sparsely distributed) justify maintaining *A. longiberbis* as a distinct species.

Andropogon longiberbis and the robust variant of *A. glomeratus* var. *pumilus* differ in many ways, the most reliable being peduncle length, raceme-sheath width, spikelet dimensions, callus-hair length, and scabrousness of the lower glume keels.

[5]Hackel cited "Florida leg. Garber, Curtiss." He apparently had at least three sheets of the first collection and one of the second (Florida, Duval County, *A. H. Curtiss 3638*, W!, FLAS!, US!) in his herbarium (the sheets are stamped "Herbarium E. Hackel"). One of the Garber sheets is here selected as the lectotype.

The possibility that *Andropogon longiberbis* is a cleistogamous derivative of ancestral stock of *A. tracyi* is discussed under that species.

About 10 percent of all the specimens of *Andropogon longiberbis* examined in this study bear vernal-flowering stems. Over 90 percent of the 29 plants flowering between February and July had charred basal leaves, indicating a recent fire and the possibility that burning stimulates flowering.

7. **Andropogon virginicus** L. Sp. Pl. 1046. 1753, not Sp. Pl. ed. 2. 1482. 1763 (= *Andropogon leucostachyus* HBK.). TYPE: America (holotype, LINN 1211.12, photo GH!). *Holcus virginicus* (L.) Steudel, Nom. Bot. ed. 2. **1:** 773. 1840, pro syn. *Sorghum virginicum* (L.) Kuntze, Rev. Gen. Pl. **2:** 792. 1891.

DIAGNOSIS. Ligules short, usually brownish and prominently ciliate margined; peduncles and spikelets short; anthers often marcescent within spikelet.

DISTRIBUTION. In more or less full sun and in all but poorest soils; extremely weedy. Massachusetts to Ontario and Michigan, south to Florida and Texas; Mexico and Central America; West Indies; Colombia; apparently naturalized in California, Hawaii, Japan, and Australia.

Andropogon virginicus is the most ubiquitous, weedy, and taxonomically complex broomsedge in the eastern United States. The old-field variant is an extraordinarily successful colonizer of moist, cleared ground at low elevations. The great variability of *A. virginicus* ties it to four of the other species of the complex: one or more of its variants resemble eight of the lowest-ranking taxa of these four species. The ancestral stock of *A. virginicus* is hypothesized to be *A. brachystachyus,* and its closest relative from a morphological standpoint is *A. longiberbis.* Finally, certain of its variants have been confused or lumped with three taxa of *A. glomeratus* and two of *A. gyrans.* These ties are considered in more detail in the discussion of these four species.

At the subspecific level there are two varieties of *Andropogon virginicus* that differ in leaf color (green vs. glaucous). At a still lower level the three variants of var. *virginicus* and the two of var. *glaucus* are so closely related to one another and are separated by such variable characters that to bring them into the formal nomenclatural scheme of the group is impractical.

The subspecific variation in this species reflects rapid and probably recent evolution. With the acquisition of the capability for cleistogamous flowering and the tremendous disturbance of the native vegetation by man has come an explosion of broomsedge populations. A possible phylogeny of this species and its closest relative, *Andropogon brachystachyus,* is discussed under the latter species.

Within *Andropogon virginicus* all of the distances between the five variants lie between 3 and 8.5 (TABLE 6). Due to the smallness of the morphological gaps between the variants of *A. virginicus,* they have all been combined into one species.

Key to the Subspecific Taxa of *Andropogon virginicus*

1. Leaves green. . . . . *A. virginicus* var. *virginicus.*
   2. Stem internodes green; leaves usually pubescent, at least on margin near collar.
      3. Raceme sheaths (1.7–)2.4–3.1(–4) mm wide; racemes (1.3–)1.5–2.3(–3) cm long; usually at least some peduncles more than 12 mm long. . . . . 7a. 1. Deceptive variant.
      3. Raceme sheaths usually more than 3.1 mm wide; some racemes longer than 3 cm; peduncles less than 12 mm long. . . . . 7a. 2. Old-field variant.
   2. Stem internodes glaucous; leaves glabrous. . . . . 7a. 3. Smooth variant.
1. Leaves glaucous. . . . . 7b. *A. virginicus* var. *glaucus.*
   4. Pubescence below raceme sheath absent; raceme sheaths (2.1–)2.6–3.8(–4.9) cm long; spikelets (2.6–)3.2–3.5(–3.9) mm long; racemes (1.4–)1.7–2.4(–3.2) cm long. . . . . 7b. 1. Drylands variant.
   4. Pubescence below raceme sheath sparse to dense; raceme sheaths (2.4–)3.2–4.8(–6) cm long; spikelets (3–)3.5–3.9(–4.4) mm long; racemes (1.5–)2–3(–4) cm long. . . . . 7b. 2. Wetlands variant.

7a. **Andropogon virginicus** L. var. **virginicus**

Cinna lateralis Walter, Fl. Carolin. 59. 1788. TYPE: presumably South Carolina (holotype, BM; photo, GH!).

Andropogon dissitiflorus Michaux, Fl. Bor. Am. **1:** 57. 1803 (as *dissitiflorum, nomen superfl.* for *Cinna lateralis* Walter and with the same type).

Andropogon vaginatus Ell. Bot. S. Carolina Georgia **1:** 148. 1816. TYPE: no indication of origin (holotype, CHARL[6]). *Andropogon virginicus* L. var. *vaginatus* (Ell.) Wood, Class-book Bot. 808. 1861. *Dimeiostemon vaginatus* (Ell.) Jackson, Index Kew. **1:** 760. 1893, *pro syn.*

Andropogon tetrastachyus Ell. Bot. S. Carolina Georgia **1:** 150. 1816. TYPE: South Carolina, Charleston (holotype, CHARL; photo, GH!). *Andropogon virginicus* L. var. *tetrastachyus* (Ell.) Hackel in DC. Monogr. Phanerog. **6:** 411. 1889. *Dimeiostemon tetrastachyum* (Ell.) Jackson, Index Kew. **1:** 760. 1893, *pro syn.* (as *tetrastachys*). *Anatherum virginicum* (L.) Sprengel subvar. *tetrastachyum* (Ell.) Roberty, Boissiera **9:** 213. 1960.

Andropogon eriophorus Scheele, Flora **27:** 51. 1844, *ex char.* Not *Andropogon eriophorus* Willd., 1805. TYPE: West Virginia, Charles Town (holotype, not seen).

Andropogon curtisianus Steudel, Syn. Pl. Glum. **1:** 390. 1854. TYPE: *M. A. Curtis s.n.* (CAEN, P,[7] not seen).

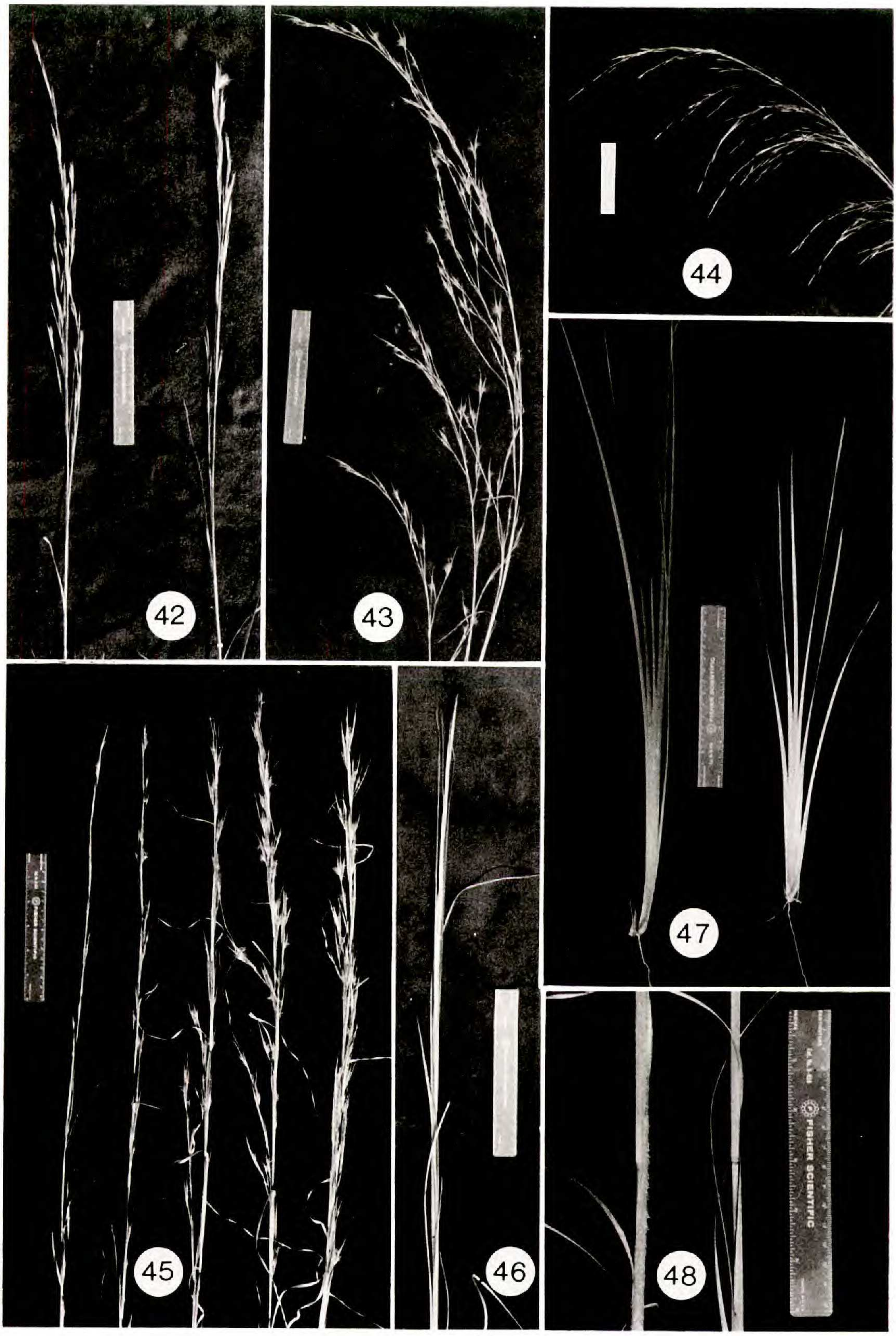
Andropogon virginicus L. subvar. *genuinus* Hackel in DC. Monogr. Phanerog. **6:** 410. 1889. *Andropogon virginicus* L. var. *genuinus* Fern. & Griscom, Rhodora **37:** 142. 1935. Both of the above names are based on *Andropogon virginicus* L.

DIAGNOSIS. Leaves green (sometimes slightly glaucous in smooth variant); racemes often more than 2 per inflorescence unit.

DISTRIBUTION. Same as species.

[6]Scribner (1901) and Weatherby (1942) placed this specimen in the taxon here recognized as *Andropogon virginicus* L. var. *virginicus.*

[7]Chase (1937) placed both of these sheets in the taxon here recognized as *Andropogon virginicus* L. var. *virginicus.*



FIGURES 42–48. 42–46, inflorescences: 42, deceptive variant of *Andropogon virginicus* var. *virginicus* (left, *Campbell 3747*) and drylands variant of *A. virginicus* var. *glaucus* (*Campbell 3898*); 43, drylands variant of *A. virginicus* var. *glaucus* (*Campbell 3865*); 44, *A. brachystachyus* (*Campbell 3884*); 45, old-field variant of *A. virginicus* var. *virginicus* (*Campbell 4144*); 46, smooth variant of *A. virginicus* var. *virginicus* (*Campbell 3902*).

7a. 1. **Old-field variant** FIGURES 11, L, M; 45.

DIAGNOSIS. Raceme sheaths wide; racemes usually 2 or more per inflorescence unit.

DISTRIBUTION. Rapidly colonizing openings in mature vegetation created by disturbance; wide variety of soils, with some capacity for ecotypic differentiation (Chapman & Jones, 1975); to about 1000 m alt. in mountains. Massachusetts to Ontario, Michigan, and Iowa, south to northern Florida and Texas; distributed sporadically south of United States; naturalized in California, Hawaii, Japan, Australia, and perhaps elsewhere (MAP 12).

REPRESENTATIVE SPECIMENS. **Canada.** ONTARIO: Kent, *Catling et al. s.n.*, 1977 (MICH). **United States.** MASSACHUSETTS: Barnstable, *Fernald 435* (DUKE, GH, MICH, MISSA, MO, NCU (2 sheets), NY, WIS); Dukes, *Kennedy s.n.*, 1896 (GH (2 sheets)); Hampshire, *Ahles 84864* (CAS); Middlesex, *French s.n.*, 1888 (MO); Nantucket, *Bicknell s.n.*, 1904 (NY). RHODE ISLAND: Washington, *Celarier A-2620-1* (MO); Newport, *Fernald et al. 8480, 8487* (GH). CONNECTICUT: Fairfield, *Eames 8723* (USF); Hartford, *Bissell s.n.*, 1901 (GH, NY); Middlesex, *Gould 8832* (TAES); New Haven, *Allen s.n.*, 1877 (GH). NEW YORK: Bronx, *Bicknell 9656* (NY); New York, *Burnham 597* (GH); Suffolk, *Latham 29538* (GA). NEW JERSEY: Atlantic, *Wagner 500* (MICH); Burlington, *Koster 05-53-2* (MICH); Cape May, *Mackenzie 6331* (DUKE, MO, NY); Middlesex, *Churchill s.n.*, 1889 (GH, MO); Ocean, *Mackenzie 2369* (MO, NY); Union, *Griscom 1500* (USF). PENNSYLVANIA: Adams, *Loughridge 2767* (TAES); Berks, *Stoudt & Hermann 2728* (MICH); Dauphin, *Berkheimer 15262* (GH); Huntington, *Westerfield 19186* (NCU); Indiana, *Feduska s.n.*, 1958 (VT); Montgomery, *Dreisbach 1150* (MICH); Philadelphia, *Brenner 8351* (GH); York, *Pohl 1463* (WIS). DELAWARE: Kent, *Larsen 309* (GH); New Castle, *Canby s.n.*, 1899 (GH); Sussex, *Larsen 465* (DUKE, GH, MO). MARYLAND: Allegany, *Brown s.n.*, 1971 (NCU); Anne Arundel, *Smith s.n.*, 1879 (US); Harford, *Smith s.n.*, 1879 (US); Kent, *Campbell 4219* (GH); Queen Annes, *Campbell 4218* (GH); Talbot, *Earle 3734* (DUKE, GH). DISTRICT OF COLUMBIA: *Chase 273* (GH, MO, NY, US (2 sheets)). WEST VIRGINIA: Barbour, *Moore 2546* (GH, MICH); Cabell, *Gilbert 807* (GH, NY, TENN, WIS); Greenbrier, *Hunnewell 7222* (GH); Hampshire, *Downs 8980* (NCU); Kanawha, *Dennison s.n.*, 1966 (TAES); Monongalia, *Millspaugh 834* (NY); Randolph, *Greenman 79* (GH). VIRGINIA: Arlington, *Allard 76* (MO); Bedford, *A. H. Curtiss s.n.*, 1872 (GH); Fauquier, *Allard 1134* (GH, NY); Frederick, *Hunnewell 11361* (GH); James City, *Menzel 334* (GH); Lunenburg, *Ahles & James 61945* (NCU); Northampton, *Fernald et al. 5187* (GH); Patrick, *Kral 9719* (NCU); Roanoke, *Wood 5742* (GH); Stafford, *Iltis 1047* (FSU). NORTH CAROLINA: Alamance, *Ramseur & Hammond 2957* (DUKE, NCU); Anson, *Correll 7105* (DUKE, GH); Bertie, *Godfrey 7004* (DUKE, GH); Buncombe, *Biltmore 21ᵈ* (GH, MO, NY); Caldwell, *Radford 19712* (DUKE, NCU); Craven, *Godfrey & White 6782* (DUKE, GH); Durham, *Blomquist 10180* (DUKE, NY); Gates, *Godfrey 7044* (DUKE, GH); Haywood, *Ahles & Duke 50305* (MISS, NCU); Hoke, *Ahles 36355* (NCU, WIS); New Hanover, *Schallert s.n.*, 1935 (DUKE, NCU); Rowan, *Small & Heller 349* (MO, NY). SOUTH CAROLINA: Aiken, *Ahles & Crutchfield 55214* (NCU); Allendale, *Bell 5204* (DUKE, NCU); Beaufort, *Bell 5249* (DUKE, NCU); Florence, *Campbell 4003* (GH); Jasper, *Bell 5293* (DUKE, NCU); Kershaw, *Radford 29927* (GH, NCU); Lee, *Radford 29382* (NCU, NY); Lexington, *Radford 29798* (GH, NCU). GEORGIA: Baker, *Thorne 6975* (GA); Bartow,

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47, *A. brachystachyus* (left, *Campbell 3884*) and drylands variant *A. virginicus* var. *glaucus* (*Campbell 3898*), basal clumps of leaves. 48, old-field (left) and smooth variants of *A. virginicus* var. *virginicus* (*Campbell 4133a, b,* St. Johns Co., Florida), stems. Scale = 15 cm.

MAP 12. Distribution of old-field variant of *Andropogon virginicus* var. *virginicus.*

Greear 63371 (GA); Bullock, *Hall 221* (NCU); Butts, *Campbell 4144* (GH); Carroll, *Campbell 4147* (GH); Clarke, *Cronquist 4208* (GA, GH, NY); Coweta, *Campbell 4145* (GH); Dade, *Cronquist 4832* (GA, GH, NY); Evans, *Hardin & Duncan 14660* (GA, MICH); McIntosh, *Duncan 20605* (DUKE, GH, US, USF, WIS); Putnam, *Cronquist 4858* (GA, GH, MICH, MO, NY); Thomas, *Campbell et al. 4057* (GH); Walker, *Cronquist 4802* (GA, GH, MICH, NY); Wayne, *Campbell 4019* (GH). FLORIDA: Alachua, *Swallen 5558* (US); Baker, *Campbell 3849* (GH); Bay, *Godfrey 61631* (DUKE, FSU, USF); Calhoun, *Godfrey 61600* (FSU, USF); Collier, *Cooley et al. 9010* (FSU, GH, TENN, USF); Dade, *Atwater GS 156* (FSU, USF); Dixie, *Godfrey 56153* (FSU, NY); Duval, *A. H. Curtiss 3636* (DUKE, GA, MISSA, MO, NCU, NY); Escambia, *Campbell 3949* (GH); Franklin, *Kral 52387* (US); Gilchrist, *Godfrey 74119* (FSU, VDB); Highlands, *Ray et al. 10370* (NCU, USF, VDB); Hillsborough, *Ray et al. 10126* (NCU, TAES, USF); Jackson, *Campbell 3770* (GH); Jefferson, *Campbell 3843* (GH); Lee, *Lakela et al. 30541* (NCU, USF); Liberty, *Campbell 4075* (GH); Martin, *Campbell 3896* (GH); Pasco, *Ray 9607* (GH, NCU, US, USF); Pinellas, *Tracy 7375* (MO, NY, W); Wakulla, *Godfrey 67525* (FSU, NCU, VDB); Walton, *Godfrey 55249* (DUKE, FSU, GA, GH, NY). MICHIGAN: Allegan, *Van Schaack s.n.,* 1945 (US); Berrien, *Parmelee 3017* (WIS); Livingston, *Kilburn 371* (MICH); Muskegon, *Bourdo 20* (MICH); Washtenaw, *Bartlett s.n.,* 1956 (MICH). OHIO: Athens, *Silby s.n.,* 1896 (NY); Cuyahoga, *Jones 1397* (TENN); Greene, *Demaree 11850* (MO, WIS); Hamilton, *Stephenson s.n.,* 1930 (GA, MO); Huron, *Jones 1270* (FSU, NCU); Pike, *Crowl s.n.,* 1937 (NY); Stark, *Brown s.n.,* 1940 (NY). INDIANA: Crawford, *Deam 30268* (US); Dariess, *Deam 7623* (US); Dearborn, *Deam 42717* (US); Franklin, *Deam 35304* (US); Lawrence, *Kriebel 1428* (DUKE); Monroe, *Duncan 271* (GA); Owen, *Deam 35013* (US); Pike, *Deam 35076* (MICH); Switzerland, *Deam 41098* (US). KENTUCKY: Bath, *Gleason & Griffiths G509b* (MICH); Butler, *Nicely 3136* (NCU); Kenton, *Braun 3752* (NY, US); Lincoln, *Wharton G584* (MO); Montgomery, *Wharton 6191* (MICH, MO, NY); Powell, *Gleason & Griffiths G173a* (MICH, NY, TENN). TENNESSEE: Blount, *Thomas s.n.,* 1965 (TENN); Coffee, *DeSelm 1994* (TENN); Fayette, *DeSelm s.n.,* 1972 (TENN); Graniger, *Cain s.n.,* 1938 (FSU, TENN, WIS); Knox, *Ruth 751* (NY); Monroe, *Sharp et al. 17048* (NCU, TENN); Morgan, *Rogers et al. 40973* (NCU, TENN); Polk, *Biltmore 21*[b] (NY, W); Roane, *DeSelm 29898* (TENN); Washington, *Armentrout s.n.*, 1961 (TENN); White, *DeSelm 216* (TENN). ALABAMA: Baldwin, *Campbell 3803a* (GH); Covington, *Kral 44748* (VDB); Houston, *Campbell 4155* (GH); Lauderdale, *Kral 29355* (GA, TENN, VDB); Lee, *Earle 4* (MO, NY); Mobile, *Mohr s.n.*, 1884 (NY, US); Montgomery, *Campbell 3956* (GH); Randolph, *Campbell 4149* (GH); Sumter, *Campbell 3955* (GH). MISSISSIPPI: Bolivar, *Ray 5990* (MISSA, USF); Covington, *Jones 10878* (MISS); Forrest, *Rogers & Robbins 4885* (NCU, VDB); Harrison, *Tracy 4698* (GH, MISS, MO, NCU, W); Jackson, *Tracy 3787* (MO, NY); Lafayette, *Pullen 641532* (GA, MISS, NCU); Lamar, *Jones 2545* (FSU, MISS, NCU); Oktibbena, *Tracy 1398* (MO, NY); Pearl River, *Sargent 8489* (MICH, MISS, US); Tishomingo, *Ray 7560* (MISSA, NCU, USF, VDB (2 sheets)). ILLINOIS: Jackson, *Bailey & Swayne* (NCU); Lawrence, *Henderson 62-1056* (FSU); Pike, *Evers 67516* (NCU); Williamson, *Voigt s.n.*, 1950 (NCU). IOWA: Wapello, *Hayden 8446* (US). MISSOURI: Boone, *Rickett 1137* (DUKE); Butler, *Eggert s.n.*, 1893 (MO); Cape Girardeau, *Steyermark 64022* (MO); Franklin, *Croat 3912* (MO); Howell, *Steyermark 20034* (MO); Madison, *Steyermark 1433* (MO); New Madrid, *Steyermark 83438* (GA); Shannon, *Redfearn et al. 844* (NCU); St. Clair, *Henderson 67-1951* (FSU, VDB); St. Louis, *Steyermark 638* (MO). ARKANSAS: Baxter, *Robinson 2242* (NY); Benton, *Plank s.n.*, 1900 (MO); Calhoun, *Demaree 22670* (MO, NY); Clark, *Demaree 21760* (MO, NCU, US); Fulton, *Robinson 2285* (NY); Grant, *Demaree 16571* (MICH, MO, NY, US); Howard, *Demaree 9706* (MO, NY); Izard, *Robinson 2135* (NY); Jefferson, *Demaree 23398* (MO, NCU, NY); Miller, *Heller 4233* (MO, NY); Randolph, *Robinson 2310* (NY); St. Francis, *Demaree 59675* (NCU); Stone, *Robinson 2328* (NY). LOUISIANA: Allen, *Ball 233* (NY); Aroyelles, *Harvey 8099* (MICH); Beauregard, *Thieret 28136* (DUKE); Calcasieu, *Shinners 22124* (WIS); Jackson, *Thomas & Cicala 31821* (NCU, TENN); Lincoln, *Garrett 87* (WIS); Morehouse, *Thomas & DePoe 440* (VDB); Ouachita, *Thomas & Jones 895* (USF, VDB); Orleans, *Hooker s.n., s.d.* (NY); St. Tammany, *Arsène et al. 11151* (NY); Vermilion, *Reese 6083* (VDB). KANSAS: Neosho, *Holland 2593* (NCU); Wyandotte, *Henderson 64-628* (FSU). OKLAHOMA: Bryan, *Taylor 7176* (VDB); Cleveland, *Nighswonger N-316* (TAES); Delaware, *Wallis 5945* (FSU, NCU, VDB); Le Flore, *Waterfall 15223* (GH); McCurtain, *Rickerson 447* (USF); Ottawa, *Wallis 8369* (FSU, NCU, VDB); Payne, *Bridge 220* (USF); Sequoyah, *Wallis 5640* (VDB). TEXAS: Angelina, *McCall 64-30* (TAES); Aransas, *Cory 51161* (MICH, NY); Bowie, *Letterman s.n.*, 1894 (MICH, MO, NY); Dallas, *Kral 447* (FSU); Ft. Bend, *Silveus 5429* (TAES); Galveston, *Waller & Bauml 3284* (GH, TAES); Gonzales, *Tharp et al. s.n.*, 1948 (DUKE, NY); Houston, *Coleman s.n.*, 1935 (TAES); Montgomery, *Gould 5399* (TAES); Newton, *Parker & Cory 10861, 10862* (TAES); Robertson, *Gould 6556* (TAES); San Jacinto, *Hartman 1280.5* (TAES); Smith, *Reverchou 2206* (MO, NY); Titus, *McGregor 706* (WIS); Tyler, *Gould 7308* (TAES); Waller, *Silveus 5118* (TAES). CALIFORNIA: Calaveras, *Bacigalupi 6087* (UC); Placer, *Crampton 5793* (TAES); Sacramento, *Crampton 5129* (TAES); Sonoma, *Yates 6865* (MO); Stanislaus, *Crampton 3025* (TAES). HAWAII: Oahu, *Correll 12307* (GH). **Mexico.** SAN LUIS POTOSÍ, *Schaffner 1049* (GH). VERACRUZ: Jalapa, *Hitchcock 274* (GH, TEX, UC, W). OAXACA: Tolusa[?], *Beetle et al. M-1362* (FLAS). CHIAPAS: La Trinitaria, *Breedlove 36962* (CAS). QUINTANA ROO: Laguna Chemkabnab, *Swallen 2771* (MICH). **Belize:** Boomtown, *O'Neill 8466* (CAS, F, GH, MICH, UC); Manatee Lagoon, *Peck 150* (GH). MORAZÁN: El Jicarito Region, *Standley 24241* (F, UC); Quebrada de Santa Clara, *Standley 22300* (F, MICH). **Guatemala.** HUEHUETENANGO: Finca San Rafael, *Steyermark 49490* (F); Miramar, *Steyermark 51535* (F). **Honduras:** Morazán, 87°W, 14°N, *Williams & Molina 17173* (GH). **Nicaragua.** MANAGUA, *Garnier 1951a* (GH). **Panama.** CANAL ZONE, *Hitchcock 8013* (CAS, MICH). PANAMÁ: Chorrera, *Hitchcock 8143* (MICH). **Bermuda:** without further locality, *Brown & Britton 225* (GH). **Greater Antilles.** CUBA. Pinar del Río: Herradura, *Ekman 14081* (US); Remartes, *Ekman 11370* (US); San Diego de los Baños, *León 5118* (GH); San Felipe, *León 15862* (GH); San Julian, *Ekman 11140* (MICH). Isla de Pinos: Los Indios, *León & Victorin 17868* (GH, US). Las Villas: Helechales, *León 5407* (GH); Soledad, *Jack 6193* (A, CAS). Oriente: Loma Mensara, *Ekman 3211* (TEX, US). JAMAICA: Appleton, *Hitchcock 9656½* (US); Bull Head Mtn., *Hitchcock 9542* (US); Cinchona, *Harris 11268* (GH, US); Claremont, *Hitchcock 275* (GH, TEX, W); Montego Bay, *Hitchcock 9680*

(US). DOMINICAN REPUBLIC: Monte Cristi, *Ekman 12771* (GH, TEX); Santo Domingo, Trujillo, *Allard 13194* (GH). **Lesser Antilles.** TRINIDAD AND TOBAGO: *Broadway 4044* (GH). **Colombia.** CHOCÓ: near Quidbo, *Gentry & Renteria 24517* (MO). **Japan.** KYUSHU: Hondo, *Togasi s.n.,* 1952 (GH, W, WIS).

This variant is named for its prominence in old-field succession in the eastern United States. The type in the Linnaean herbarium apparently represents one part of this variant, and it is the basis of the common concept of *Andropogon virginicus.* The variant includes two kinds of plants that are so close they cannot be distinguished either in the field or in the herbarium with great confidence, although their extremes differ somewhat in height, inflorescence thickness, and number of racemes per inflorescence unit. I have seen the two kinds growing together in northern Florida and in North Carolina, where they are barely distinguishable.

The deceptive variant may also closely resemble the old-field variant. The former has narrower raceme sheaths and a peduncle that occasionally exceeds 10 mm in length. These two variants are more easily separated in the field than the two kinds of plants of the old-field variant, but a similar uncertainty about herbarium material still prevails.

7a. 2. **Deceptive variant** FIGURES 11, N; 42.

DIAGNOSIS. Raceme sheaths narrow; peduncles sometimes greater than 10 mm long; racemes usually 2.

DISTRIBUTION. Flatwoods, scrublands, disturbed sites (e.g., cleared timberlands). Coastal Plain from North Carolina to Florida (MAP 16).

REPRESENTATIVE SPECIMENS. **United States.** VIRGINIA: Isle of Wight, *Fernald & Long 12568* (GH, US); Nansemond, *Fernald & Long 10943* (DUKE, GH, US). NORTH CAROLINA: Bertie, *Campbell 4223* (GH); Bladen, *Campbell 4208* (GH); Dare, *Fosberg 17875* (MICH); Duplin, *Blomquist & Correll 4819* (GH); Martin, *Radford 41798* (WIS); Nash, *Godfrey & Kerr 6621* (DUKE). SOUTH CAROLINA: Beaufort, *Cuthbert s.n.,* 1886 (FLAS); Berkeley, *Ahles 35450* (NCU); Clarendon, *Campbell 4222* (GH); Jasper, *Bell 4813* (NCU). GEORGIA: Brantley, *Campbell 4229* (GH); Calhoun, *Thorne 6903* (GH); Clinch, *Eyles 397* (MO); Long, *Bozeman 1944* (GA); McIntosh, *Duncan 20643* (WIS); Thomas, *Campbell 3922* (GH), Tift, *Shepherd 341* (TAES). FLORIDA: Alachua, *Campbell 4186* (GH); Baker, *Godfrey 74698* (FSU); Bay, *Billington s.n.,* 1921 (MICH); Brevard, *Fredholm 6193* (US); Calhoun, *Godfrey 75791* (FSU); Charlotte, *Lakela 24675* (FLAS, GH); Clay, *Swallen 5583, 5598, 5614* (US); Collier, *Lakela 31155* (GA, USF); Dade, *Silveus 6620* (DUKE); Duval, *A. H. Curtiss 3639d* (GH); Franklin, *Campbell 3931* (GH); Gulf, *Chapman s.n., s.d.* (GH); Highlands, *Campbell 3747* (GH); Hillsborough, *Lakela 26662* (GH); Indian River, *Tracy 9257* (TAES, US); Jackson, *Campbell 4081* (GH); Jefferson, *Campbell & Godfrey 4068* (GH); Lake, *Campbell 4197* (GH); Lee, *Hitchcock 441* (MO); Leon, *Godfrey & Campbell 4230* (GH); Liberty, *Campbell et al. 4168* (GH); Manatee, *Tracy 7107* (MO, NY, W); Martin, *Campbell 3870* (GH); Nassau, *Godfrey 74699* (FLAS); Okeechobee, *West 23* (FLAS); Pinellas, *Davis s.n., s.d.* (FLAS); Polk, *Lakela 23585* (GH, US); Putnam, *Godfrey 76896* (FSU); St. Lucie, *Silveus 6665* (TAES); Sarasota, *McFarlin & Van Dyne 12037* (US); Seminole, *Chase 4137* (US); Walton, *Godfrey 75763* (FSU).

This variant is so named because of its deceiving similarity to three other taxa, the old-field variant of *Andropogon virginicus* var. *virginicus, A. glomeratus* var. *hirsutior,* and the robust variant of *A. glomeratus* var. *pumilus.*

MAPS 13–16. Distribution of some subspecific taxa of *Andropogon virginicus*: 13, var. *glaucus*, wetlands variant; 14, var. *glaucus*, drylands variant; 15, var. *virginicus*, smooth variant; 16, var. *virginicus*, deceptive variant.

Discussion of the distinguishing characteristics of the deceptive variant is provided under each of these taxa.

The deceptive variant does not correspond to any taxon for which a name has been published. Its discovery has been crucial to an understanding of

Andropogon virginicus because the variant appears to be both the primitive member of the species and the evolutionary link to *A. brachystachyus*.

7a. 3. **Smooth variant** FIGURE 48.

DIAGNOSIS. Like old-field variant but with glaucous stems and glabrous leaves.

DISTRIBUTION. Poorly drained soils (e.g., shallow ponds, swales, cut-over flatwoods); much less common than old-field variant. Coastal Plain from North Carolina to Mississippi (MAP 15).

REPRESENTATIVE SPECIMENS. **United States.** NORTH CAROLINA: Bladen, *Campbell 4213* (GH). GEORGIA: Brantley, *Campbell 4202* (GH); Wayne, *Campbell 4228* (GH). FLORIDA: Alachua, *Campbell 4232* (GH); Brevard, *Fredholm 6109* (GH, US); Franklin, *Godfrey 77363* (FSU); Gulf, *Chapman s.n., s.d.* (GH); Highlands, *Campbell 3902* (GH); Indian River, *Tracy 9759* (TAES); Jackson, *Campbell 3785* (GH); Leon, *Godfrey 74595* (FSU, VDB); Liberty, *Godfrey 75790* (FSU); Martin, *Campbell 4129* (GH); St. Johns, *Campbell 4227* (GH); Volusia, *Silveus 6736* (TAES); Wakulla, *Godfrey & Morar 61570* (FSU); Walton, *Campbell 3787* (GH). ALABAMA: Baldwin, *Campbell 3803b* (GH). MISSISSIPPI: Jackson, *Tracy 2276* (NY).

The smooth variant does not correspond to any taxon for which a name has been published. It is a glaucous-stemmed, glabrous-leaved derivative of the old-field variant that has a narrower tolerance for soil moisture conditions. From a limited number of observations of progeny of these two taxa, there is no evidence that they are genetic segregates of one another.

7b. **Andropogon virginicus** L. var. **glaucus** Hackel in DC. Monogr. Phanerog. **6:** 411. 1889. TYPE: Florida, Duval County, *A. H. Curtiss 3638b* (holotype, W!; isotypes, GA (two sheets)!, GH!, MISSA!, MO!, US!). FIGURES 11, O; 42; 43; 47.

Andropogon virginicus L. var. *dealbatus* Hackel[8] in DC. Monogr. Phanerog. **6:** 411. 1889. TYPE: Alabama, Mobile County, *Mohr 1884* (holotype, W!).
Andropogon capillipes Nash, Bull. New York Bot. Gard. **1:** 431. 1900. Based on *Andropogon virginicus* L. var. *glaucus* Hackel. Not *Andropogon glaucus* Retz., 1789, or *Andropogon glaucus* Muhl., 1817.

DIAGNOSIS. Leaves glaucous; racemes 2, rarely 3.

DISTRIBUTION. Moist or dry soils on Coastal Plain. Southern New Jersey to eastern Texas (MAPS 13, 14).

The diagnoses and distributions of the drylands and wetlands variants of this taxon are included in the comparative discussion of the two taxa.

REPRESENTATIVE SPECIMENS.
Drylands variant. **United States.** NORTH CAROLINA: Brunswick, *Blomquist 10442* (DUKE); New Hanover, *Chase 4582* (US). SOUTH CAROLINA: Allendale, *Campbell 4015* (GH). GEORGIA: Brantley, *Campbell 4025* (GH); Echols, *DeSelm 1969* (TENN); Ware, *Campbell*

[8]Hackel's *Andropogon virginicus* L. vars. *glaucus* and *dealbatus* are united here for the first time. The former varietal name is used here to preserve common usage.

3708 (GH); Wayne, *Campbell 4020* (GH). FLORIDA: Bay, *Godfrey 76131* (FSU); Brevard, *Fredholm 6128* (GH, MO, US); Calhoun, *Ford 5642* (FLAS, NCU, W); Citrus, *DeSelm 1969* (TENN); Collier, *Lakela 31192* (GH, MO, NCU); Columbia, *Silveus 6749* (DUKE, GA, TAES); Dade, *Silveus 5284* (TAES, VT); DeSoto, *DeSelm s.n.*, 1969 (TENN); Dixie, *Godfrey 56152* (FSU, GH, NY, USF); Duval, *A. H. Curtiss 36386* (GA, GH, MISSA, MO, US); Franklin, *Godfrey 74585* (FSU, NCU, VDB); Glades, *McCart 11190* (USF); Gulf, *Silveus 6742a* (GA, TAES, US); Hamilton, *Godfrey 74648* (FSU, NCU, VDB); Highlands, *Brass 15632* (GH, US); Hillsborough, *Lakela 23614* (US, USF); Jackson, *Campbell et al. 4165* (GH); Jefferson, *Godfrey 75828* (FSU); Lafayette, *Godfrey 76906* (FSU); Lake, *Ray 10543* (GH, US); Lee, *Stanley 12536* (US); Liberty, *Campbell 3827* (GH); Marion, *Campbell 4196* (GH); Martin, *Campbell 3898* (GH); Okaloosa, *Godfrey 68900* (FSU); Okeechobee, *McCart 11120* (USF); Orange, *Anderson 4085* (FSU); Osceola, *Campbell 3865* (GH); Palm Beach, *Davis s.n.*, 1941 (GH); Pinellas, *Tracy 7377* (GH, MO, NY, TAES, US, W, WIS); St. Johns, *Godfrey 74716* (FSU); St. Lucie, *Silveus 6660* (TAES, US); Seminole, *Beardslee 43* (US); Wakulla, *Godfrey 74591* (FLAS, FSU, NCU, VDB). ALABAMA: Baldwin, *Kral 38250* (GA, VDB); Covington, *Kral 44730* (VDB).

Wetlands variant. **United States.** NEW JERSEY: Cape May, *Long 5145* (NY). NORTH CAROLINA: Bladen, *Ashe s.n., s.d.* (NCU, NY); Brunswick, *Blomquist 405* (DUKE, NY); Cumberland, *Ahles 36571* (NCU). GEORGIA: Bullock, *Campbell 4018* (GH); Colquitt, *Godfrey 76085* (FSU); Harris, *Jones 22259* (GA); Long, *Bozeman & Radford 1943* (NCU). FLORIDA: Bay, *Godfrey 76135* (FSU); Bradford, *Conde s.n.*, 1977 (FLAS); Charlotte, *DeSelm s.n.*, 1969 (TENN); Clay, *Campbell & Godfrey 4136* (GH); Collier, *Cooley et al. 9062* (FSU, GH, USF); Columbia, *Ashe s.n.*, 1929 (NCU); Dixie, *Godfrey 69228* (FSU); Duval, *A. H. Curtiss 6055* (GH, TAES); Escambia, *Silveus 6756* (TAES, VT); Gulf, *Chapman s.n., s.d.* (GH, MO, NY); Hillsborough, *Combs 1346a* (US); Indian River, *Tracy 9284* (TAES, US); Jackson, *Campbell 3912* (GH); Lee, *Wunderlin et al. 5399* (USF); Leon, *Godfrey 75786* (FSU); Liberty, *Campbell 3820* (GH); Pasco, *Ray 9596* (USF); Putnam, *Godfrey 74721* (FSU, NCU, VDB); Santa Rosa, *Godfrey 76185* (FSU); Walton, *Campbell 3940* (GH); Wakulla, *Godfrey & Morar 61570a* (DUKE, FLAS, FSU, USF); Washington, *Campbell 3938* (GH). ALABAMA: Baldwin, *Campbell 3800* (GH); Butler, *Kral 44702* (VDB); Geneva, *Kral 41714* (GH, USF, VDB); Mobile, *Mohr s.n.*, 1884 (NY, US, W). MISSISSIPPI: Forrest, *Rogers & Robbins 4884-B* (MISS); Harrison, *Tracy 3897* (MO, NY, TAES); Jackson, *Tracy 3814* (TAES). LOUISIANA: Calcasieu, *Thieret 27991* (FSU); Livingston, *Rogers 2419-A* (MISS, NCU); Rapides, *Duvall 6019* (TAES); St. Mary, *Silveus 5406* (TAES). TEXAS: Galveston, *Waller 3316* (GH, TAES); Houston, *Lindheimer s.n.*, 1841 (MO).

The pattern of small morphological differences associated with ecological differences of *Andropogon virginicus* var. *virginicus* reappears in the pair of taxa comprising *A. virginicus* var. *glaucus*. The drylands variant of *A. virginicus* var. *glaucus* produces generally shorter raceme sheaths, racemes, and spikelets; its flowers are more frequently chasmogamous, and unlike the wetlands variant, it has no hairs below the raceme sheath. In addition, it grows in better-drained soil and has a narrower geographic range.

In the majority of instances, these morphological and soil-moisture differences are correlated. I have seen these taxa growing within one to three meters of one another at three localities in northwestern Florida. At only one of these was there difficulty in classifying any individual: a single plant on a slope between a bog inhabited by the wetlands variant and a roadside lined with the drylands variant combined the morphological features of these two taxa. The cause of this morphological intermediacy is unknown.

The strong overlap in the characters separating the drylands and wetlands variants and the breakdown in the correlation of these characters in about five percent of all populations examined in the herbarium are the reasons these two taxa are not recognized nomenclaturally.

Hackel (1889) suggested that the drylands variant of *Andropogon virginicus* var. *glaucus* is closely related to ("vergit ad") *A. brachystachyus.* In inflorescence morphology the two are sometimes similar because larger plants of the drylands variant usually produce arching branches (FIGURE 43); they also share a preference for well-drained soils. They differ in stem height, in glaucousness, in peduncle, spikelet, and anther length, and in anther color. It is possible that *A. brachystachyus* stock is ancestral to the drylands variant, but the deceptive variant of *A. virginicus* var. *virginicus* is a more likely ancestor of the drylands variant because there is an even closer resemblance between these two. Apart from glaucousness, they differ in raceme-sheath length and in pubescence below the raceme sheath.

Since the deceptive and wetlands variants differ from the drylands variant in the same characters, it is not surprising that the first two taxa are morphologically alike. In addition to glaucousness, the wetlands variant differs from the deceptive variant in its larger raceme sheaths, wider range, and tolerance of more soil moisture.

Leaves of the wetlands variant are sometimes faintly glaucous, even on healthy plants. If such plants are not examined carefully, they may be mistaken for a plant of the smooth variant with inflorescence units with only two racemes.

8. **Andropogon brachystachyus** Chapman, Fl. So. U. S. ed. 2. 668. 1883. TYPE:[9] Florida, Duval County, *A. H. Curtiss 3632* (lectotype, US!; isolectotypes, DUKE!, FSU!, GA!, GH!, MO (two sheets)!, NCU!, US!). *Sorghum brachystachyum* (Chapman) Kuntze, Rev. Gen. Pl. **2:** 791. 1891. *Anatherum brachystachyum* (Chapman) G. Roberty, Boissiera **9:** 212. 1960.
FIGURES 11, G; 44; 47.

DIAGNOSIS. Stems tall; leaves long, sparsely pubescent; inflorescence branches long, arching (in herbarium specimens inflorescences appear rather open); racemes and awns short; spikelets and anthers long.

DISTRIBUTION. Sandy, often seasonally wet soils of flatwoods, savannas, pond margins, and scrublands. Southern Georgia and Florida (MAP 3).

REPRESENTATIVE SPECIMENS. **United States.** GEORGIA: Brantley, *Campbell 4022* (GH); Chatham, *Eyles 6652* (US); Long, *Bozeman 1908* (NCU); Wayne, *Campbell 4021* (GH). FLORIDA: Alachua, *Silveus 6519* (TAES, US); Baker, *Ashe s.n.*, 1928 (NCU); Brevard, *Fredholm 5558* (GH, MO, US); Clay, *Harper 40* (GH, MO, US); Collier, *Lakela 30327* (GH, NCU, NY, USF); Columbia, *DeSelm s.n.*, 1969 (TENN); Dixie, *Godfrey 56183* (FSU, GA, GH, USF); Duval, *A. H. Curtiss 5338* (GA, GH, US); Highlands, *Campbell 3884* (GH); Indian River, *Tracy 9285* (TAES, US); Jefferson, *Godfrey 74602* (FSU, NCU, VDB); Lafayette, *Godfrey 74632* (FSU, VDB); Lake, *Nash 1193* (GH, MO, NY, TAES, US); Leon, *Godfrey 74594* (FSU, VDB); Levy, *Godfrey et al. 64751* (FSU, VDB); Madison, *Godfrey 75831* (FSU); Marion, *Campbell 4195* (GH); Martin, *Campbell 3897* (GH); Nassau, *Godfrey 74680* (FSU, NCU, VDB); Okeechobee, *McCart 11121* (USF); Orange, *Baker 39* (GH, NY); Osceola, *Campbell*

[9]The lectotypification of Hitchcock (1951) is followed here.

3864 (GH); Pasco, *Ray 9588* (GH, NCU, USF, VDB); Pinellas, *Tracy 7376* (GH, MO, NY, TAES, US); Polk, *Lakela 23584* (US, USF); Putnam, *Godfrey 74720* (FSU, NCU); Seminole, *Beardslee 46* (US); St. Johns, *Godfrey 74719* (FSU, NCU, VDB); Taylor, *Godfrey 74634* (FSU, NCU, VDB); Volusia, *Hood 65* (US).

The combination of elongate, arching inflorescence branches, long peduncles, and short racemes makes *Andropogon brachystachyus* very distinctive. Its closest relative is the deceptive variant of *A. virginicus* var. *virginicus.* These two taxa are separated by a morphological distance of 8 (TABLE 6). The deceptive variant may be a cleistogamous derivative of ancestral stock of *A. brachystachyus.*

One population of *Andropogon brachystachyus* in Long County, Georgia (*Campbell 4021*), on the northern edge of this taxon's range, suggests that one of its ancestors might have given rise to the deceptive variant. Most of the plants in this population are characteristic of *A. brachystachyus*: they are tall (average, 2 m; range, 1.57–2.17 m); the branches arch; the peduncles range from 20 to 40 mm long; the spikelets exceed 4 mm in length; and the anthers are more than 1.9 mm long. Two individuals, however, are shorter (average, 1.4 m) and have erect to only slightly arching branches, peduncles less than 13 mm, spikelets less than 3.8 mm, and anthers less than 1.4 mm. As peduncle, spikelet, and anther length suggest, there is a greater frequency of cleistogamous flowers at the base of the racemes of these two individuals than in the rest of the population. These changes may be the product of mutation in regulatory genes hastening sexual maturity. The importance of these plants is that they are strikingly similar to the deceptive variant of *A. virginicus* var. *virginicus.* Because of its smaller size, erect branches, shorter peduncles, and longer racemes, the deceptive variant has a much different appearance than plants of *A. brachystachyus* (except the anomalous individuals of the Long County population). In less conspicuous ways, however, they are very alike. They have the same ligule morphology, amount and distribution of leaf pubescence, and stem internode color. They differ, however, in three nonmorphological ways. First, in peninsular Florida the deceptive variant flowers two to four weeks before *A. brachystachyus,* although at the northern limit of the range of *A. brachystachyus,* their flowering periods overlap. Second, the deceptive variant is more frequently cleistogamous. Third, *A. brachystachyus* may form large, dense populations, but it does not invade disturbed sites as does the deceptive variant. It seems plausible that the deceptive variant arose from *A. brachystachyus* stock as a precociously flowering form. This paedomorphosis (Gould, 1977) may be reflected in the earlier flowering time of the deceptive variant and, through the introduction of cleistogamy, may have provided the deceptive variant with a breeding system that is adaptive for a colonizer.

9. **Andropogon glomeratus** (Walter) B.S.P. Prelim. Catal. Anthophyta Pteridophyta New York, 66. 1888. Based on *Cinna glomerata* Walter, Fl. Carolin. 59. 1788. TYPE: South Carolina (holotype, BM, not seen; fragment, NY!; photo, GH!). *Sorghum glomeratum* (Walter) Kuntze, Rev. Gen. Pl. **2:** 790. 1891. *Anatherum virginicus* (L.) Sprengel subvar. *glomeratus* (Walter) G. Roberty, Boissiera **9:** 212. 1960.

Andropogon macrourus Michaux, Fl. Bor. Am. 56, 57. 1803, *nomen superfl.* for *Cinna glomerata* Walter and with same type. *Andropogon spathaceus* Trin. Fund. Agrost. 186. 1820, *nomen nudum,* placed in synonymy of *Andropogon macrourus* Michaux by Steudel, Nomencl. Bot. ed. 2. **1:** 93. 1840. *Anatherum macrourum* (Michaux) Griseb. Mem. Am. Acad. II. **8:** 534. 1864, as *macrurum. Dimeiostemon macrourus* (Michaux) Jackson, Index Kew. **1:** 760. 1893, *pro syn.*, as *macrurum.*

DIAGNOSIS. Stem sheaths scabrous (smooth in taxon 9c, often in 9d); leaf blades long; ligules long, light brown, short-ciliate (often short and with long ciliations in taxon 9d); inflorescences oblanceolate to obpyramidal, usually with at least 3 branches at 1 or more stem nodes; inflorescence units numerous.

DISTRIBUTION. Poorly drained soils; throughout entire range of virginicus complex. Only *Andropogon glomeratus* var. *pumilus* extends beyond eastern United States to western United States, Mexico, Central America, West Indies, and South America.

Of the five taxa included in *Andropogon glomeratus,* three (vars. *glomeratus, hirsutior,* and *glaucopsis*) are particularly close to one another morphologically and ecologically. Besides the characters given in the species diagnosis, these three varieties have ligules that are identical in their length, short-ciliate margins, and color. *Andropogon glomeratus* var. *glomeratus* appears to be the most primitive of the three because of its frequent chasmogamous flowering (as expressed in the long peduncles and large anthers). It also generally has larger spikelets than the mostly cleistogamous vars. *hirsutior* and *glaucopsis.* Finally, inflorescence shape can be used to separate var. *glomeratus* from the other two taxa. Although the distance between vars. *glomeratus* and *hirsutior* is only 4 (TABLE 6), the characters separating them are usually consistent and clear.

In Virginia and the Carolinas, where individuals of vars. *glomeratus* and *hirsutior* may infrequently have similar peduncle lengths, one must rely upon inflorescence shape, spikelet and anther length, and flowering mode for identification.

While the stem sheaths of vars. *glomeratus* and *hirsutior* are scabrous, pubescent (at least near the collar), and green, those of var. *glaucopsis* are smooth, glabrous, and glaucous. Glaucousness (uncommon in the complex, in sect. LEPTOPOGON, and in the genus as a whole) is the basis for the conjecture that var. *glaucopsis* is derived, probably from var. *hirsutior* stock. FIGURE 49 shows the hypothesized phylogeny of these three taxa.

The greatest problem within *Andropogon glomeratus* is the affinity of the robust variant of var. *pumilus.* In the past either it has not been recognized or it has been given the status of species, variety, or form. Morphologically, it is clearly farther from any of the first three taxa of the species than each of these is from any other. As discussed for vars. *glomeratus* and *hirsutior,* the robust variant may often appear very similar to them in general appearance. Characters of stem-sheath and glume-keel scabrousness and ligule morphology distinguish the robust variant and place the southwestern variant of var. *pumilus* in between the robust variant and the rest of *A. glomeratus.* The morphological inter-

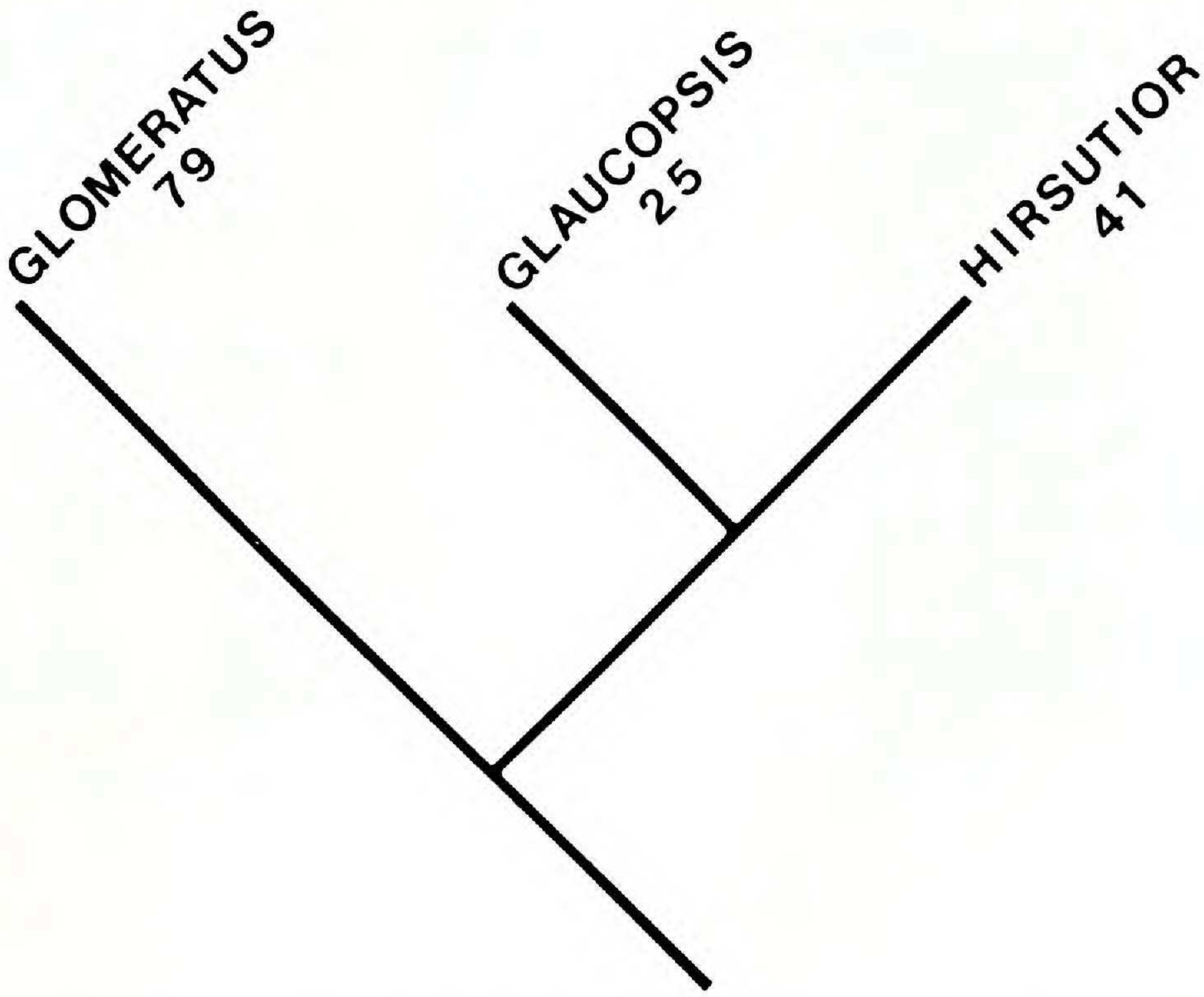


FIGURE 49. Hypothesized phylogeny of *Andropogon glomeratus* vars. *glomeratus*, *hirsutior*, and *glaucopsis*. Numbers below names indicate mean percent chasmogamy (character 33 of TABLE 6).

mediacy of the southwestern variant unites the robust variant and vars. *glomeratus, hirsutior*, and *glaucopsis*.

Key to the Subspecific Taxa of *Andropogon glomeratus*

1. Leaves glaucous. .... 9c. *A. glomeratus* var. *glaucopsis*.
1. Leaves green.
   2. Raceme sheaths usually less than 2.5 mm wide; stem sheaths often smooth; ligules usually less than 1 mm long, often with long-ciliate margins. .... 9d. 1. Robust variant of *A. glomeratus* var. *pumilus*.
   2. Raceme sheaths usually more than 2.5 mm wide; stem sheaths often rough; ligules usually more than 1 mm long, with short-ciliate margins.
      3. Keels of lower glume scabrous to well below middle; plants of southwestern United States and northwestern Mexico. .... 9d. 2. Southwestern variant of *A. glomeratus* var. *pumilus*.
      3. Keels of lower glume scabrous only above middle; plants of eastern United States.
         4. Inflorescences (linear-)oblong; spikelets usually less than 4 mm long; anther usually marcescent within spikelet; peduncles less than 10 mm long; plants of Coastal Plain from Maryland to Mississippi. .... 9b. *A. glomeratus* var. *hirsutior*.
         4. Inflorescences oblong to obpyramidal; spikelets usually more than 4 mm long; anther usually not marcescent within spikelet; usually some mature

peduncles more than 10 mm long; plants of Coastal Plain and well inland from Massachusetts to Mississippi. . . 9a. *A. glomeratus* var. *glomeratus.*

9a. **Andropogon glomeratus** (Walter) B.S.P. var. **glomeratus**

FIGURES 11, S; 53.

Andropogon macrourus Michaux var. *abbreviatus* Hackel in DC. Monogr. Phanerog. **6:** 408. 1889. TYPE:[10] Carolina, *Rugel s.n.*, 1841 (lectotype, W!). *Andropogon glomeratus* (Walter) B.S.P. var. *abbreviatus* (Hackel) Scribner, U. S. D. A. Div. Agrost. Bull. 7(ed. 3): 15. 1900. *Andropogon corymbosus* (Hackel) Nash var. *abbreviatus* (Hackel) Nash in Britton, Man. Fl. No. States Canada, 70. 1901.

Andropogon macrourus Michaux var. *corymbosus* Hackel in DC. Monogr. Phanerog. **6:** 409. 1889. TYPE: Florida, Duval County, *A. H. Curtiss 3639c* (holotype, W!; isotypes, FLAS!, GH (2 sheets)!, NCU, US!) (*N.B.: Curtiss 3639c* of GA! and MISSA! are taxon 9d). *Andropogon glomeratus* (Walter) B.S.P. var. *corymbosus* (Hackel) Scribner, U. S. D. A. Div. Agrost. Bull. 7(ed. 3): 15. 1900. *Andropogon corymbosus* (Hackel) Nash in Britton, Man. Fl. No. States Canada, 69. 1901. *Andropogon virginicus* L. var. *corymbosus* (Hackel) Fern. & Griscom, Rhodora **37:** 142. 1935.

DIAGNOSIS. Inflorescences oblong to obpyramidal; peduncles and spikelets usually long; stamens not regularly marcescent within spikelets.

DISTRIBUTION. Bogs, swamps, savannas, flatwoods, and ditches. Massachusetts to Kentucky and Arkansas, south to Florida and Louisiana (MAP 17).

REPRESENTATIVE SPECIMENS. **United States.** MASSACHUSETTS: Barnstable, *Fernald et al. 14984* (GH); Bristol, *Sturtevant s.n.*, 1888 (MO); Dukes, *Seymour 1441* (DUKE, GH, NY); Nantucket, *William s.n.*, 1894 (GH); Plymouth, *Blake 11425* (MICH, US). RHODE ISLAND: Washington, *Collins & Lownes s.n.*, 1923 (GH). NEW YORK: Nassau, *Bicknell 9643* (NY); Richmond, *Britton s.n.*, 1879 (NY); Suffolk, *Smith 3495* (MO, WIS). NEW JERSEY: Atlantic, *Letterman s.n.*, 1887 (MICH, MO); Burlington, *MacElwee 1571* (GH, MO, NY); Camden, *Stewart 3052* (NY); Gloucester, *Fosberg 14488* (DUKE); Middlesex, *Miller 1077* (NY); Monmouth, *Britton s.n.*, 1883 (NY); Ocean, *Morton 40931* (VDB); Passaic, *Nash s.n.*, 1899 (NY). PENNSYLVANIA: Berks, *Brumbach 353-34* (GH); Chester, *Pennell 8890* (NY); Fayette, *Boardman s.n.*, 1941 (VT); Lancaster, *Carter s.n.*, 1910 (NY); Philadelphia, *Van Pelt s.n.*, 1906 (GH). DELAWARE: Kent, *Goodale 62538* (GH); Sussex, *Churchill s.n.*, 1908 (MO). MARYLAND: Baltimore, *Freeman s.n.*, 1874 (WIS); Harford, *Wilkins 5709* (GH); Howard, *Foreman s.n.*, 1873 (NY); Prince Georges, *True 2879* (DUKE, GA, US); Worcester, *Campbell 3983* (GH). DISTRICT OF COLUMBIA: *Hitchcock 256* (GH, MO, NY, USF, W). WEST VIRGINIA: Cabell, *Millendor s.n.*, 1939 (US); Raleigh, *Berkley 2253* (US). VIRGINIA: Accomac, *Fernald et al. 5577* (GH); Appomattox, *Kral 11179* (NCU); Augusta, *Massey 3101* (NCU); Isle of Wight, *Fernald & Long 5759* (GH); James City, *Grimes 3874* (NY); Northampton, *Fernald & Long 5183* (GH); Southampton, *Campbell 4217* (GH); Surry, *Terrell 4368* (NCU). NORTH CAROLINA: Allegheny, *Blomquist & Anderson 925* (DUKE); Bertie, *Ahles & Haesloop 52066* (NCU); Bladen, *Ahles 37431* (NCU); Brunswick, *Bartram s.n.*, 1922 (GH); Buncombe, *Biltmore 920*[b] (MO, NCU, NY); Cherokee, *Radford 17577* (NCU); Chowan, *Ahles & Duke 51029* (NCU); Columbus, *Bell 15740* (NCU); Craven, *Godfrey & White 6835* (GH); Cumberland, *Ahles & Leisner 33534* (NCU); Currituck, *Blomquist 14382* (DUKE); Davidson, *Denke s.n.*, 1826 (DUKE); Gates, *Godfrey 7037* (GH); Halifax,

[10]Hackel cited "New Jersey (Gray); South Carolina (Rugel)." The 1841 collection of Rugel from "Carolina" is here designated as the lectotype rather than Rugel's 1842 collection from "Carolina" (W!). I have not seen material of Gray from New Jersey that Hackel would have seen.

FIGURES 50–55. 50–54, inflorescences: 50, *Andropogon glomeratus* var. *hirsutior* (*Campbell 3851*); 51, robust variant of *A. glomeratus* var. *pumilus* (*Campbell 4030*); 52, southwestern variant of *A. glomeratus* var. *pumilus* (*Crampton 6710,* Yolo Co., California (UC)); 53, *A. glomeratus* var. *glomeratus* (*Campbell 3915*); 54, *A. glomeratus* var. *glaucopsis* (*Campbell 3812*). 55, *A. glomeratus* var. *glaucopsis* (*Campbell 3812*), basal clumps of leaves. Scale = 15 cm.

MAPS 17–19. Distribution of some subspecific taxa of *Andropogon glomeratus*: 17, var. *glomeratus*; 18, var. *hirsutior*; 19, var. *glaucopsis*.

Ahles & Leisner 20846 (FSU, NCU); Harnett, *Laing 381* (NCU); Henderson, *Hunnewell 10084* (GH); Hertford, *Ahles & Haesloop 52210* (NCU); Hoke, *Correll 7184* (DUKE, GH); Jackson, *Correll 7903* (DUKE); Johnston, *Radford 29217* (NCU); Jones, *Radford 40022* (NCU); Lee, *Stewart s.n.*, 1958 (NCU); Macon, *Anderson s.n.*, 1953 (DUKE, FSU, GH); Martin, *Radford 41831* (NCU); Moore, *Blomquist 277* (DUKE); Nash, *Ahles & Leisner 21259* (NCU, VDB); Onslow, *Wilder 17676* (DUKE); Orange, *Ashe s.n., s.d.* (NY); Pamlico, *Radford 42286* (NCU); Pender, *Wells s.n.*, 1925 (NY); Pitt, *Radford 41604* (NCU); Richmond, *Radford 19355* (NCU); Robeson, *Britt 2506* (WIS); Sampson, *Campbell 4000* (GH); Scotland, *Godfrey 6964* (GH); Transylvania, *Freeman 56938* (NCU); Tyrrell, *Radford 42535* (NCU); Wake, *Ashe s.n., s.d.* (NCU); Warren, *Ahles & Bell 21837* (NCU); Washington, *Radford 42352* (NCU); Wayne, *Burk s.n.*, 1958 (NCU); Yancey, *Freeman 58353* (NCU). SOUTH CAROLINA: Aiken, *Ravenel s.n., s.d.* (NY); Anderson, *Davis 7919* (MO); Barnwell, *Batson & Kelley s.n.*, 1952 (NCU); Berkeley, *Ahles 35461* (NCU); Clarendon, *Campbell 4005* (GH); Dorchester, *Ahles & Haesloop 37783* (NCU); Hampton, *Bell 5351* (NCU); Lexington, *Radford 29889* (FSU, NCU); Pickens, *Rodgers 246* (DUKE); Sumter, *Holdaway 46* (DUKE). GEORGIA: Bartow, *Duncan 13268* (GA, GH); Emanuel, *Plummer & Pullen s.n.*, 1962 (NCU); Forsyth, *Duncan 9028* (GA); Irwin, *Harper 1709* (GH, MO, NY); Rabun, *Duncan 1047* (GA); Thomas, *Campbell 3921* (GH); Toombs, *Hardin & Duncan 14585* (NCU); Ware, *Campbell 4142* (GH). FLORIDA: Alachua, *Godfrey & Morrill 52620* (FSU); Bay, *Godfrey 61628* (FSU, VDB); Brevard, *Fredholm 6197* (GH, US); Columbia, *Ashe s.n.*, 1929 (NCU); Duval, *A. H. Curtiss 3639c* (FLAS, GH, NCU, US, W); Escambia, *Campbell 3950* (GH); Gulf, *Chapman s.n.*, 1893 (NY); Jackson, *Campbell 3915* (GH); Jefferson, *Godfrey 75826* (FSU); Lake, *Campbell 4109* (GH); Leon, *Kral 1801* (FSU, GH); Liberty, *Campbell 4073* (GH); Orange, *Meislahn 53* (US); Polk, *Jennings s.n.*, 1931 (USF); Putnam, *Godfrey 76895* (FSU); Santa Rosa, *Godfrey 76192* (FSU); Wakulla, *Godfrey 72248* (FSU). KENTUCKY: Casey, *Braun 2680* (US); Laurel, *Braun s.n.*, 1933 (US); McCreary, *Rogers 37* (GA, GH, MICH, MO, NY); Montgomery, *Wharton 5375* (GH, MICH, NY); Rowan, *Braun 2085* (US). TENNESSEE: Bledsoe, *Shanks et al. 3555* (NCU, TENN); Blount, *Sharp et al. 32416* (TENN, VDB); Coffee, *DeSelm et al. s.n.*, 1963 (NCU); Cumberland, *Shanks & Norris 7304* (TENN, US); Fentress, *Shanks 3076* (TENN, VDB); Grundy, *Kral 44545* (VDB); Morgan, *Shanks 3062* (TENN); Polk, *Clebsch 20217* (NCU, TENN). ALABAMA: Baldwin, *Campbell 3805* (GH); Cullman, *Eggert s.n.*, 1897 (MO, NY, US); Jackson, *Chase 4488* (US); Lee, *Earle & Baker s.n.*, 1897 (MO); Mobile, *Sargent s.n.*, 1941 (US); Pike, *Leland s.n., s.d.* (GH). MISSISSIPPI: Forrest, *Rogers 4735* (MISS); Greene, *Rogers 2509* (TENN); Harrison, *Tracy 4699* (MICH, NCU, NY, TAES, W); Jackson, *Tracy 3802* (MICH, MO); Lamar, *Sargent 144* (GH); Pearl River, *Amacker s.n.*, 1938 (MISSA); Tishomingo, *Anonymous s.n.*, 1937 (MISSA). ARKANSAS: Pulaski, *Engelmann 80* (MO); Saline, *Moore 321117* (WIS).

Andropogon glomeratus var. *glomeratus* is not as aggressive a colonizer as its two hypothetical derivatives, *A. glomeratus* vars. *hirsutior* and *glaucopsis*. Plants in the northern part of the range of var. *glomeratus* tend to be of shorter stature and to have shorter peduncles.

Andropogon glomeratus var. *glomeratus* and the robust variant of var. *pumilus* have inflorescences so similar in shape that most previous workers have united them and have overlooked the differences between them. The robust variant is taller, usually with rather smooth sheaths and with shorter, more ciliate, and darker ligules, narrower raceme sheaths, and lower glume keels that are scabrous below the middle. Although both taxa grow in wet sites, the robust variant is weedier, shows a greater tolerance for drier conditions and various soil types, and has a wider geographic range.

9b. **Andropogon glomeratus** (Walter) B.S.P. var. **hirsutior** (Hackel) Mohr, Bull. Torrey Bot. Club **24:** 21. 1897. Based on *Andropogon macrourus* Michaux var. *hirsutior* Hackel in DC. Monogr. Phanerog. **6:** 409. 1889. TYPE: Alabama, Mobile County, *Mohr s.n.*, 1884 (holotype, W!). *Andropogon virginicus* L. var. *hirsutior* (Hackel) Hitchc. Jour. Wash. Acad.

Sci. **23:** 456. 1933. *Andropogon virginicus* L. var. *tenuispatheus* (Nash) Fern. & Griscom f. *hirsutior* (Hackel) Fern. & Griscom, Rhodora **37:** 142. 1935. FIGURES 11, Q; 50.

DIAGNOSIS. Inflorescences (linear)-oblong; peduncles and usually spikelets short; stamens usually marcescent within spikelet.

DISTRIBUTION. Ditches, swales, bogs, flatwoods, and savannas, often forming very large populations in cleared, low ground. Coastal Plain from Maryland to Mississippi (MAP 18).

REPRESENTATIVE SPECIMENS. **United States.** MARYLAND: Somerset, *Hermann 9973* (GH, NY). VIRGINIA: Greensville, *Kral 14297* (USF); Isle of Wight, *Fernald & Long 6760* (GH, NY); Nansemond, *Fernald & Long 10944* (US); Northampton, *Fernald et al. 5181* (GH, NY, USF); Southampton, *Campbell 4216* (GH); Sussex, *Fernald & Long 7308* (GH). NORTH CAROLINA: Bertie, *Godfrey 7006* (GH); Bladen, *Ashe s.n., s.d.* (NCU); Brunswick, *Bell 16247* (NCU); Chowan, *Ahles & Duke 51035* (USF); Craven, *Godfrey & White 6768* (GH); Cumberland, *Ahles 36560* (NCU); Duplin, *Ahles 35747* (GH, NCU); Greene, *Radford 40434* (NCU, VDB); Halifax, *Ahles & Leisner 20845* (FSU, NCU, USF); Hertford, *Ahles & Haesloop 52210* (NCU); Hoke, *Correll 7181* (UC); Hyde, *Fosberg 17744* (MICH); Johnston, *Radford 29144* (NCU, USF); Lenoir, *Radford 31591* (NCU); Nash, *Godfrey & Kerr 6623* (GH, MO); Pitt, *Radford 41741* (NCU); Richmond, *Radford 19335* (NCU); Robeson, *Ahles 37253* (NCU); Sampson, *Campbell 3996* (GH); Tyrrell, *Radford 42553* (NCU); Wayne, *Burk s.n.*, 1958 (NCU); Wilson, *Radford 40781* (NCU). SOUTH CAROLINA: Bamberg, *Ahles 37658* (NCU); Chesterfield, *Radford 18679* (NCU); Clarendon, *Radford 30899* (NCU); Darlington, *Coker s.n.*, 1909 (NCU); Jasper, *Campbell 3964* (GH). GEORGIA: Berrien, *Celarier s.n.*, 1953 (MO); Brantley, *Campbell 4024* (GH); Colquitt, *Godfrey 76081* (FSU); Grady, *Komarek s.n.*, 1977 (FSU); Terrell, *Duncan 1772* (GA); Thomas, *Campbell et al. 4058* (GH); Ware, *Campbell 4141* (GH). FLORIDA: Alachua, *Chase 4216* (MICH); Baker, *Campbell 3851* (GH); Clay, *Campbell 4199* (GH); Duval, *A. H. Curtiss 3639b* (GA, MISSA, MO); Hillsboro, *Combs 1358* (US); Jackson, *Campbell 3810* (GH); Jefferson, *Godfrey 75830* (FSU); Lake, *Campbell 4131* (GH); Liberty, *Campbell 4074* (GH); Leon, *Silveus 6710-B* (GA, TAES); Madison, *Godfrey 75833* (FSU); Martin, *Campbell 3875* (GH); Orange, *Combs & Baker 1134* (NY); Polk, *Jennings s.n.*, 1923 (USF); Santa Rosa, *Godfrey 76803* (FSU); Seminole, *Hood s.n.*, 1911 (MO); Wakulla, *Godfrey 76239* (FSU); Walton, *Godfrey 75762* (FSU). ALABAMA: Baldwin, *Campbell 3804* (GH); Mobile, *Mohr s.n.*, 1896 (NCU); Washington, *Kral 49069* (VDB). MISSISSIPPI: Harrison, *Tracy 4699* (MO).

Earlier workers failed to appreciate the great similarity of *Andropogon glomeratus* vars. *hirsutior* and *glaucopsis* probably because they overlooked the numerous similarities in overall size, inflorescence appearance, and ligule morphology, as well as in morphological characters associated with the predominantly cleistogamous flowering mode. The varieties are also remarkably alike in geographic distribution and ecological preferences. They colonize extensively, much more so than their closest relative, *A. glomeratus* var. *glomeratus*, and form very dense populations in the moist, cleared ground of recently harvested timberlands. Often the two grow together in populations of thousands of individuals.

Because they grow together so frequently and are morphologically so alike, the possibility that they are not distinct taxa but merely genetic segregates of one another has been carefully considered. Based on observations of several hundred seedlings grown from seeds from both taxa (growing together in nature), there is no evidence for genetic segregation. The glaucousness/greenness and pubescence/glabrousness of the stem sheaths are discernible in the seedlings within a few weeks of germination. (Stem-sheath scabrousness often does not develop in the greenhouse in var. *hirsutior.*) The seedlings consistently match their parents in these two characters.

These taxa are unusual in the virginicus complex because their morphological differences are not associated with differences in either ecology or geography. The two taxa are recognized as varieties within the virginicus complex because they are more easily distinguished from one another than are the variants.

Andropogon glomeratus var. *hirsutior* resembles three other taxa besides *A. glomeratus* vars. *glomeratus* and *glaucopsis.* It has long been confused with individuals of the robust variant of *A. glomeratus* var. *pumilus* with a narrow inflorescence. The two can be distinguished by sheath scabrousness, ligule morphology, raceme-sheath width, peduncle length, and lower-glume-keel scabrousness. *Andropogon glomeratus* var. *hirsutior* is narrower in both ecological preference and geographic range than the robust variant. A closer morphological similarity exists between var. *hirsutior* of the southeastern United States and the southwestern variant of var. *pumilus.* Indeed, the differences (ligule margin, lower-glume scabrousness, and sometimes inflorescense denseness) are small and are not always easily discerned. Finally, in general aspect, var. *hirsutior* and the deceptive variant of *A. virginicus* var. *virginicus* are very close. They are separated by stem-sheath scabrousness and ligule morphology.

9c. **Andropogon glomeratus** (Walter) B.S.P. var. **glaucopsis** Mohr, Bull. Torrey Bot. Club **24:** 21. 1897. Based on *Andropogon macrourus* Michaux var. *glaucopsis* Ell. Bot. S. Carolina Georgia **1:** 149, 150. 1816. TYPE: South Carolina, *Elliott 181* (holotype, CHARL, not seen; isotype,[11] PH!). *Andropogon glaucopsis* (Ell.) Nash in Small, Fl. SE. U. S. 63. 1903. *Andropogon virginicus* L. var. *glaucopsis* (Ell.) Hitchc. Am. Jour. Bot. **21:** 139. 1934. FIGURES 11, R; 54; 55.

Andropogon glaucus Muhl. Descr. uber. Gramin. 278. 1817. Not *Andropogon glaucus* Retz., 1789. TYPE: South Carolina, *Elliott 181* (holotype, CHARL, not seen; isotype, PH!). *Cymbopogon glaucus* (Muhl.) Schultes, Mant. Syst. Veg. **2:** 459. 1824.

DIAGNOSIS. Stem sheaths smooth; leaves glabrous, glaucous; racemes short.

DISTRIBUTION. Flatwoods, bogs, ditches, swamps, pond margins, and swales. Coastal Plain from southern Virginia to Mississippi (MAP 19).

REPRESENTATIVE SPECIMENS. **United States.** VIRGINIA: Princess Anne, *Fernald & Griscom 2765* (GH, USF). NORTH CAROLINA: Bertie, *Campbell 3991* (GH); Bladen, *Ahles 37350* (NCU); Carteret, *Phipps et al. 3688* (NCU); Craven, *Ahles & Duke 51035* (NCU); Dare, *Blomquist 8081* (GH); Greene, *Radford 40373* (NCU, UC); Jones, *Radford 39837* (NCU); New Hanover, *Canby s.n.,* 1867 (NY); Onslow, *Moldenke 122* (NY); Pamlico, *Godfrey & White 6813* (GH); Pender, *Ahles 36208* (NCU); Sampson, *Campbell 3995* (GH); Wake, *Ashe s.n., s.d.* (MO); Wayne, *Radford 31503* (NCU). SOUTH CAROLINA: Chesterfield, *Radford 18679* (NCU); Dorchester, *Ahles & Haesloop 37784* (NCU); Georgetown, *Radford*

[11]Smith (1962) equated the Elliott specimen at PH to the specimen with the same number at CHARL.

31379 (GA, NCU); Horry, *Duke 0064* (NCU); Jasper, *Campbell 3963* (GH). GEORGIA: Brantley, *Campbell 4023* (GH); Camden, *Duncan & Hardin 14390* (NCU); Charlton, *Harper 693* (NY); Chatham, *Mellinger s.n.*, 1958 (GH); Lowndes, *Quarterman 5345* (VDB); McIntosh, *Duncan 20673* (GH, MICH, NCU, USF, WIS); Thomas, *Campbell 4229* (GH); Tift, *Shepard 220* (TAES); Ware, *Silveus 5368* (TAES); Wayne, *Campbell 4205* (GH). FLORIDA: Alachua, *Godfrey & Morrill 52618* (FSU); Baker, *Godfrey 74664* (FSU, NCU, VDB); Bay, *Godfrey 76141* (FSU); Brevard, *Shuey & Poppleton 1540* (USF); Clay, *Campbell 4200* (GH); Columbia, *Combs & Rolf 128* (US); Dixie, *Godfrey 56176* (FSU, GA, NY, USF); Duval, *A. H. Curtiss 6077* (GA, GH, MO, NY); Franklin, *Godfrey 71208* (FSU); Highlands, *Brass 14612* (GH); Indian River, *Tracy 9255* (TAES); Jackson, *Campbell 3812* (GH); Jefferson, *Godfrey 74599* (FSU, NCU, VDB); Lafayette, *Godfrey 74631* (FSU, NCU); Lake, *Campbell 4132* (GH); Leon, *Campbell & Godfrey 4062* (GH); Liberty, *Campbell 4072* (GH); Madison, *Kral 3760* (FSU, GH, NCU); Manatee, *Tracy 7735* (GH, MO, NY, TAES, W, WIS); Martin, *Campbell 4128* (GH); Orange, *Campbell 3908* (GH); Osceola, *Ray et al. 10493* (USF); Pasco, *Ray 9605* (GH, NCU, USF); Polk, *McFarlin 3747* (MICH); Putnam, *Silveus 6743* (LA, TAES); Santa Rosa, *Godfrey 76798* (FSU); Taylor, *Kral 52127* (VDB); Volusia, *Hood s.n.*, 1911 (GA); Wakulla, *Godfrey 64977* (FSU, VDB). ALABAMA: Baldwin, *Campbell 3806* (GH); Mobile, *Iltis et al. 21367* (WIS). MISSISSIPPI: Harrison, *Demaree 36240* (FSU, MISSA, TAES, VDB); Jackson, *Caldwell 368* (FSU).

Andropogon glomeratus var. *glaucopsis* and both the drylands and wetlands variants of *A. virginicus* var. *glaucus* have been combined by some authors (Nash, 1912) and confused by many botanists. *Andropogon glomeratus* var. *glaucopsis* differs from *A. virginicus* var. *glaucus* in its longer ligules and leaves and can be distinguished from the drylands variant by its pubescence below the raceme sheath, its inflorescence shape, and its habitat. Although these three differences do not hold for var. *glaucopsis* and the wetlands variant, the former has shorter raceme sheaths and racemes than the latter.

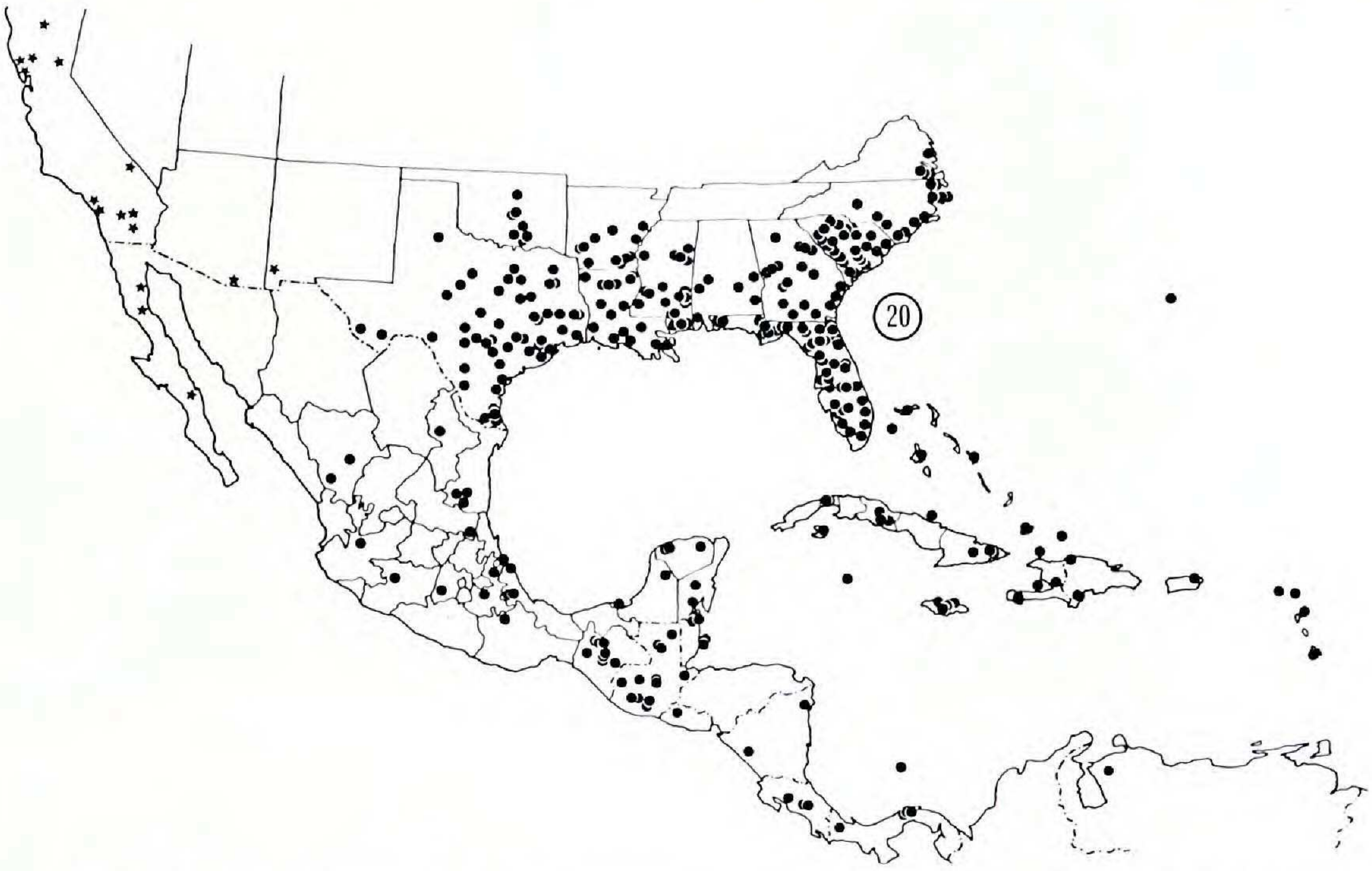
9d. **Andropogon glomeratus** (Walter) B.S.P. var. **pumilus** Vasey, Bot. Gaz. **16:** 27. 1891. TYPE: Texas, Val Verde County, *Neally 256*, 1890 (holotype, US, not seen; isotype, UC!, W!).

Andropogon glomeratus (Walter) B.S.P. var. *tenuispatheus* Nash in Small, Fl. SE. U.S. 61. 1903. TYPE:[12] Florida, Duval County, *A. H. Curtiss 5337*, 1894 (lectotype, NY!; isolectotypes, GA (two sheets)!, GH!, NY!, W!). *Andropogon tenuispatheus* (Nash) Nash, N. Am. Fl. **17:** 113. 1912. *Andropogon virginicus* L. var. *tenuispatheus* (Nash) Fern. & Griscom, Rhodora **37:** 142. 1935. *Andropogon virginicus* L. var. *hirsutior* (Hackel) Hitchc. f. *tenuispatheus* (Nash) Fern. & Griscom, Rhodora **42:** 416. 1940. *Anatherum virginicum* (L.) Sprengel subvar. *tenuispatheum* (Nash) G. Roberty, Boissiera **9:** 213. 1960.

DIAGNOSIS. Keels of lower glumes often scabrous to below middle.

DISTRIBUTION. Moist, disturbed sites (e.g., roadsides, fresh or brackish swamps, swales, moist woods, and fields). Virginia to California and south; extremely common through Mexico and Central America to northern South America; common throughout West Indies (MAP 20).

[12]One of the many specimens annotated by Nash and at NY has been selected as the lectotype.



MAP 20. Distribution of *Andropogon glomeratus* var. *pumilus* (dots, robust variant; stars, southwestern variant).

9d. 1. **Robust variant** FIGURES 11, P; 51.

DIAGNOSIS. Stem sheaths usually smooth; ligules usually short; raceme sheaths narrow.

DISTRIBUTION. See distribution under variety for ecological preferences of this variant. One of most aggressive and ubiquitous weeds in North America. Throughout distribution of variety except southwestern United States and northwestern Mexico (MAP 20).

REPRESENTATIVE SPECIMENS. **United States.** VIRGINIA: Isle of Wight, *Fernald & Long 13887* (GH, MO, NY); Middlesex, *Hermann & Martin s.n.*, 1939 (MICH, NY, TENN); Nansemond, *Fernald et al. 15197* (GH, NY); Norfolk, *Fernald & Griscom 2766* (GH, USF). NORTH CAROLINA: Beaufort, *Blomquist 8027* (DUKE, NY); Brunswick, *Blomquist & Correll 4866* (DUKE, GA); Camden, *Campbell 3984* (GH); Carteret, *Blomquist 10201* (FSU, GH); Hyde, *Radford 42624* (NCU, VDB); Robeson, *Ahles 37323* (NCU); Scotland, *Sharp 2008* (NCU). SOUTH CAROLINA: Abbeville, *Radford 30739* (NCU); Beaufort, *Bell 5264* (NCU); Calhoun, *Ahles 35328* (NCU); Charleston, *Duncan 5775* (GA); Chester, *Bell 10050* (NCU); Jasper, *Campbell 3965* (GH); Kershaw, *Radford 29957* (NCU); Laurens, *Bell 10105* (NCU); McCormick, *Radford 30717* (GH, NCU); Spartanburg, *Bell 10372* (NCU). GEORGIA: Berrien, *Celarier A-2600-1* (MO, UC); Clarke, *Duncan 286* (GA); Clinch, *Faircloth & Cribbs 5003* (GA, MO, NCU); Harris, *Jones 22345* (GA, GH); McIntosh, *Duncan 20634* (GH, NCU, USF, WIS); Pike, *Duncan 3064* (GA, MICH, USF); Putnam, *Cronquist 4759* (GA, GH, MO, NY); Thomas, *Campbell et al. 4055* (GH); Sumter, *Harper 651* (NY); Washington, *Duncan 4342* (GA, MISS). FLORIDA: Alachua, *D'Arcy 2166* (GA, VDB, WIS); Baker, *Campbell 3850* (GH); Broward, *Stimson 852* (FSU, NCU, USF); Citrus, *Godfrey 65108* (FSU); Collier, *Lakela 27803* (GA, USF); Dade, *Gill s.n.*, 1970 (GH, MO, USF); Duval, *A. H. Curtiss 6078* (GA, GH, MO, NCU, NY); Escambia, *Hansen 2349* (FSU, WIS); Franklin, *Godfrey 71124* (FSU); Highlands, *Campbell 4117* (GH); Hillsboro, *Perdue 1748* (FSU, GH, NCU, TAES, UC, USF); Jackson, *Campbell 4030* (GH); Leon, *Wooten 2320* (FSU, VDB); Liberty, *Godfrey 55529* (FSU); Madison, *Godfrey 74115* (FSU, NCU, VDB); Manatee, *Perdue 1788* (FSU, GH, NCU, TAES, UC); Monroe, *Campbell 3730* (GH); Nassau, *Godfrey 74691* (FSU, VDB); Osceola, *Fredholm 6106* (GH, MO, US); Palm Beach, *Kral 5690* (FSU, VDB); Pinellas, *Deam 2767* (MO, NY); Santa Rosa, *Meriläinen & Roe 912* (NCU, WIS); St. Johns, *Ward 2305* (FSU, GH, NCU, USF, VDB); Taylor, *Godfrey 74145* (FSU, NCU, VDB). ALABAMA: Baldwin, *Campbell 3801* (GH); Barbour, *Campbell 4152* (GH); Lee, *Jones s.n.*, 1959 (GA, NCU); Marshall, *Golden s.n.*, 1974 (VDB); Mobile, *Tracy s.n.*, 1896 (MISSA); Montgomery, *Campbell 3958* (GH); Sumter, *Jones 1730* (NCU). MISSISSIPPI: Bolivar, *Temple 4669* (MISS, NCU); Clarke, *Jones 10711* (MISS); Hancock, *Demaree 36318* (FSU, GA, GH, MISSA, NCU, TAES, VDB); Harrison, *Demaree 34532* (NCU, USF, VDB); Jackson, *Demaree 34429* (FSU, NCU, TAES, USF, VDB); Jasper, *Jones 10851* (MISS); Jefferson, *McDougall 1171* (US); Lauderdale, *Campbell 3954* (GH); Oktibbeha, *Tracy s.n.*, 1890 (MISSA, NY, TAES); Warren, *Colvin s.n.*, 1938 (MISSA); Wayne, *Campbell 3952* (GH). ARKANSAS: Ashley, *Demaree 18562* (GH, MO, NY, WIS); Bradley, *Demaree 21820* (GA, MO, NY); Desha, *Demaree 21627* (NY, TENN, UC, WIS); Garland, *Demaree 46698* (TAES); Howard, *Demaree 45229* (TAES); Phillips, *Palmer 26645* (GH, MO); Pike, *Demaree 9979* (GH, MO, NY, UC, USF); Saint Francis, *Demaree 59675* (TENN, VDB). LOUISIANA: Bienville, *Sharpe 480* (USF); Caddo, *Thomas & Overby 32838* (NCU); Concordia, *Thomas & DePoe 510* (NCU, TENN); East Baton Rouge, *McCoy s.n.*, 1952 (NY); Iberia, *Delahoussaye 158* (VDB); Jackson, *Kral 16073* (FSU, VDB); Natchitoches, *Palmer 8865* (MO, NY); Orleans, *Ewan 18792* (GH, MO); West Carroll, *Demaree 14096* (GH, MO, NY); Vermilion, *Reese 3906* (FSU, GH, NCU). OKLAHOMA: Cleveland, *Goodman 2362* (GH, MO, NY); Johnston, *Waterfall 5685* (MO, NY); Marshall, *Goodman 7389* (UC, WIS); *McLain, Massey, & Hoisington 1491* (NCU); Murray, *Hopkins 1121* (MO); Payne, *Gay 130* (USF); Pontotoc, *Robbins 3202* (NY, TAES, UC). TEXAS: Anderson, *Gould 7285* (TAES); Austin, *Parks & Cory 17704* (GH, TAES); Fort Bend, *Anderwald s.n.*, 1949 (TAES); Brazos, *Beason 8* (TAES); Caldwell, *Plank 2* (TAES); Camp, *Turner 13-F* (TAES); Dallas, *Reverchon 3440* (GH, MO, NY); DeWitt, *Riedel s.n.*, 1941 (MO); Fayette, *Plank s.n.*, 1893 (NY); Freestone, *Kral 82* (FSU); Galveston, *Waller & Bauml 3159* (GH, TAES); Gonzales, *Tharp & Barkley 13006* (GH, NY, UC, VDB); Gregg, *York s.n.*, 1941 (GH, NY); Hidalgo, *Clover 462* (MICH); Karnes, *Johnson 1107* (TAES); Kerr, *Cory 52397* (GH, MICH, NY, UC); Motley, *Parks & Cory 15964* (GH, TAES); Real, *Cory 24353* (GH); Tarrant, *Whitehouse 17320* (MICH, NY); Tom Green, *Cory 5103* (GH); Uvalde, *Parks & Cory 7501* (TAES); Walker, *Cory 50637* (MICH, NY); Wharton, *Palmer 6629* (MICH, MO). **Mexico.** CHIHUAHUA: Río Bonito, *LeSueur 0100* (CAS, GH, TEX, UC). COAHUILA: Las Delicias, *Stewart 2818* (GH). NUEVO LEÓN: Cola de Caballo, *Beetle M-414* (FLAS); Monterrey, *Smith M593* (TEX). TAMAULIPAS: El Limón, *Kenoyer & Crum 3611* (GH, MICH); Gd. Wanteon, *Harvey & Witherspoon 9214* (MICH); Jaumave, *Stanford et al. 2359* (CAS, GH). DURANGO: Coyotes, *Maysilles 8294* (MICH, TEX, UC); Durango, *Palmer 251* (F, GH, MICH, UC). SAN LUIS POTOSÍ: Tamazunchale, *Edwards 944* (TEX), *Fisher 37133* (GH), *Kenoyer A597* (F, MICH). JALISCO: Guadalajara, *Palmer 466* (GH, UC, W); Villa Corona, *McVaugh 14415* (MICH). MICHOACÁN: Volcán Parícutin, *Hakala s.n.*, 1946 (MICH). HIDALGO: Jacala, *Kral 24887* (VDB). MÉXICO: Ixtapan de la Sal, *Harvey 8661* (MICH). PUEBLA: Cotimehuaca, *Arsène 3542* (GH); El Carrizal, *Pineda s.n.*, 1968 (CAS, MICH), *Arsène 1433* (GH), *Nicolas s.n.*, 1909 (GH). VERACRUZ: Cordoba, *Matuda 330* (MICH, VT), *Bourgeau 1666* (GH), *Cyasto 330* (VT); Jalapa, *Gould 9261* (MICH, TEX); Nautla, *Beetle M-1265* (WIS); Papantla, *Gutierrez s.n.*, 1967 (CAS, MICH); Orizaba, *Seaton 111* (F, GH), *Müller 2033* (W); San Salvador de Acajete, *Sharp 45622* (GH). OAXACA: San Antonio, *Smith 960* (F), *Pringle 5565* (GH, VT). CHIAPAS: Chanal, *Kaplan 126ch57* (F); Ixtapa, *Laughlin 1076* (CAS); La Trinitaria, *Breedlove 41938* (CAS); Ocozocoantla de Espinosa, *Breedlove 37797* (CAS); Pueblo Nuevo Solistahuacan, *Lathrop 5215* (CAS), *Breedlove 19931* (CAS); Rayon, *Breedlove 10159* (CAS, F); San Cristobal, *Breedlove 11915* (F, MICH); Tenejapa, *Breedlove 10926* (MICH, TEX), *Ton 1041* (F, MICH); Teopisca, *Breedlove 10545* (CAS, TEX); Venustiano Carranza, *Laughlin 1989* (CAS); Yerba Buena, *Mill 572* (CAS); Zinacantan, *Laughlin 2258* (CAS). CAMPECHE: Bolonchen de Rejon, *Gould 12626* (UC); Carmen, *Kral 25422* (MICH, VDB), *Rzedowski 26384* (CAS, F, MICH, TEX). YUCATÁN: Progreso, *Swallen 2911* (MICH); Sisal, *Gould 12641* (UC); Tizimín, *Gould 12652* (UC). QUINTANA ROO: Lake Chichancanab, *Swallen 2729* (MICH); Coba, *Lundell 7835* (MICH); Payo Obispo, *Dampf s.n.*, 1925 (F). **Belize:** Buttonwood Cay, *Fosberg & Spellman 54411* (F); Corozal, *Lundell 4902* (CAS, GH, MICH, TEX), *Gentle 134* (MICH); Honey Camp, *Lundell 428* (F, GH, US); Southwest Cay Is., *Fosberg & Stoddard 53860* (US); Tower Hill Estate, *Karling 55* (F). **Guatemala.** ALTA VERAPAZ: Cobán, *Molina s.n.*, 1963 (F); Tamahu, *Standley 70928* (F). ESCUINTLA: between Escuintla and Santa Lucía Cotz[umalguapa], *Standley 63414* (F). HUEHUETENANGO: Cuilco, *Steyermark 50800* (F, US); Ixcan, *Steyermark 49337a* (F). IZABAL: Cristina, *Blake 7570* (US), *Steyermark 38479* (F). EL PETÉN: La Libertad, *Lundell 3482* (GH, MICH, US); Tikal, *Contreras 86* (F, TEX). SACATEPÉQUEZ: Antigua, *Standley 64695* (F). SOLOLÁ: Volcán Atitlán, *Steyermark 47475* (F); Volcán San Pedro, *Steyermark 47187* (F). **El Salvador:** Matapán, *Boden s.n.*, 1900 (MO). **Nicaragua:** Managua, *Garnier 818* (MICH); Puerto Cabezas, *Pederson s.n.*, 1968 (WIS). **Costa Rica:** Cartago, *Weston et al. 3471* (UC); Puntarenas, *Pohl & Davidse 10794* (UC); San José, *Hitchcock 8465* (MICH), *Pohl & Davidse 11433* (UC). **Panama:** Barro Colorado Is., *Woodworth & Vestal 542* (F, GH); Canal Zone, *Hitchcock 8033* (US), *Standley 31228* (US); Chiriquí, *McCorkle C-53* (FSU). **Bermuda:** *Manuel 776* (GH). **Bahama Islands:** Andros, *Northrup 659* (GH); Cat Is., *Byrne 297* (GH, WIS); Grand Bahama, *Correll 40635* (TEX), *Correll & Kral 42899* (VDB); Great Inagua, *Dunbar 234* (GH); South Bimini, *Howard 10208* (GH). **Turks and Caicos Islands:** Caicos Is., *Correll 43117* (GH). **Greater Antilles.** CUBA. Habana: Cajio, *León 14697* (GH); Santiago de las Vegas, *Wilson 2207* (MICH, W). Las Villas: Manajanabo, *León 5302* (GH); Sancti-Spiritus, *León 3024* (GH); Soledad, *Howard 6230* (GH, US). Isla de Pinos: Nueva Gerona, *A. H. Curtiss 294* (GH), *Killip 44531* (US). Camagüey: Cayo Romano, *Shafer 2614* (GH). Oriente: Moa, *Bristol 191* (GH); Monte Verde, *Wright 1555* (GH); Sierra de Nipe, *Ekman 6376* (MICH). JAMAICA: Manchester, *Webster & Proctor 5252* (GH, MICH); Port Antonio, *Maxon & Killip 288* (US); St. Thomas, *Crosby et al. 825* (GH, TEX, UC). HAITI: Île de la Tortue, *Ekman 4263* (GH, US); Morne des Commissaires, *Holdridge 1324* (MICH, TEX); Port au Prince, *Beech 2048* (US), *Potter 5008* (GH); Sur Cayer, *Ekman 72* (US). DOMINICAN REPUBLIC: Barahona, *Howard 8584* (GH), *Fuentes 1281* (GH); Leybo Province, Puenta Icacos, *Ekman 15787* (GH, TEX). PUERTO RICO: Isla Verde, *Blomquist 11758* (UC). GRAND CAYMAN: *Brunt 1656* (FLAS, NCU). **Lesser Antilles.** ST. KITTS: *Hitchcock 16361* (US). ANTIGUA: *Box 128* (US). GUADELOUPE: *Questel 1422* (US), *Duss 3548* (US). MARTINIQUE: *Duss 1301* (US). **Colombia:** San Andros Is., *Gentry s.n.*, 1967 (WIS). **Venezuela.** FALCÓN: *Wingfield 5417* (MO).

The robust variant is a remarkably aggressive colonizer in a wide variety of soils. It does not characteristically invade old fields and cleared timberlands with the regularity of *Andropogon virginicus* or other taxa of *A. glomeratus*. Instead, it prefers some flow of water in the soil and often chokes roadside ditches with its dense growth (FIGURE 27).

In the greenhouse and the experimental garden it has consistently been the fastest-growing member of the virginicus complex. In the field it produces the thickest stems and the largest leaves. It appears to have some adaptations for very rapid growth, but at the same time it is phenotypically plastic in plant height. Under poorer conditions its stems may be very short, although the inflorescence remains densely and profusely branched.

The robust variant tolerates a greater range of soil salinity and pH than do other members of the virginicus complex. It grows in either brackish or fresh water and in soils derived from either acidic or alkaline rocks.

The uniquely wide ecological preferences and geographic range and the distinctive morphology of this variant argue for species ranking. On the other hand, certain individuals are very similar in general appearance to *Andropogon glomeratus* vars. *glomeratus* and *hirsutior*. The ways in which the variant differs from these two varieties have been discussed under the varieties. Furthermore, the next taxon forms a bridge between the robust variant and the rest of *A. glomeratus*, which makes the species large but coherent.

Small or shaded plants of the robust variant may resemble the deceptive variant of *Andropogon virginicus* var. *virginicus* in overall size and inflorescence shape. The two taxa differ in stem-sheath pubescence, peduncle length, and lower-glume-keel scabrousness.

9d. 2. **Southwestern variant** FIGURE 52.

DIAGNOSIS. Stem sheaths always scabrous; ligules long; spikelets often exceeding 4 mm in length.

DISTRIBUTION. Moist soils of seepage slopes and edges of springs. Utah to California, south to northwestern Mexico (MAP 20).

REPRESENTATIVE SPECIMENS. **United States.** NEW MEXICO: Grant, *Wright 2100* (GH, MO, NY, UC). ARIZONA: Santa Cruz, *Barr 63-504* (USF). NEVADA: no locality given, *Wheeler s.n.*, 1871 (GH). CALIFORNIA: Inyo, *Thorne & Tilforth 42512* (NY); Los Angeles, *Moxley 632* (MO, UC); Marin, *Howell s.n.*, 1939 (NY, UC); Placer, *Crampton 5802* (TAES); Riverside, *Reed 2901* (CAL, LA); San Bernardino, *Roos 5023* (NY, UC); Shasta, *Bacigalupi 2387* (GH); Ventura, *Pollard s.n.*, 1946 (MO, NY, UC); Yolo, *Beetle 4691* (TAES, UC, WIS). **Mexico.** BAJA CALIFORNIA NORTE: Cerro la Encantada, *Chambers 544* (CAS, UC); Santa María, *Moran 11492* (CAS, UC). BAJA CALIFORNIA SUR: Mission de San Pedro Martin Valley, *Wiggins 9036* (GH).

In the past this variant has been called *Andropogon glomeratus*. It is distinguished here for the first time as a morphologically and geographically isolated group of populations of *A. glomeratus* var. *pumilus*. Its chief taxonomic significance is that it shares some features (sheath scabrousness and ligule length) with the first two varieties of *A. glomeratus*, and others (peduncle length and scabrousness of the lower glumes) with the robust variant; it thus holds the species together. It appears to be closest to the robust variant because the two variants share the unique feature of scabrousness of the lower glume keels, a character generally more conspicuous in the southwestern variant. Their occurrence in the western United States and their preference for seepage conditions are further bases for combining them into one variety. Finally, while United States populations are fairly easily separated from the rest of var. *pumilus*, some populations in northern Mexico are more or less intermediate between the two variants. More collections and especially more field work in this area will be necessary to assess how these variants interact.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge the following people for help through exchange of ideas or critical readings of parts of this work: P. D. Cantino, E. A. K.

Coombs, M. J. Donoghue, M. W. Frohlich, C. W. Greene, C. H. Haufler, W. S. Judd, N. G. Miller, R. C. Rollins, B. G. Schubert, E. A. Shaw, S. A. Spongberg, P. F. Stevens, E. L. Taylor, R. M. Tryon, and C. E. Wood, Jr.

I also wish to thank Mike Canoso, Walter Kittredge, and the staff of the Harvard University Herbaria for the administration of herbarium loans, and the curators of the following herbaria (abbreviations follow Holmgren & Keuken, 1974) for sending loans: Botanical Museum and Herbarium, Copenhagen (C); Charleston Museum (CHARL); California Academy of Sciences (CAS); Duke University (DUKE); Field Museum of Natural History (F); University of Florida (FLAS); Florida State University (FSU); University of Georgia (GA); University of California at Los Angeles (LA); University of Michigan (MICH); University of Mississippi (MISS); Mississippi State University (MISSA); Missouri Botanical Garden (MO); University of North Carolina (NCU); New York Botanical Garden (NY); Philadelphia Academy of Natural Sciences (PH); Texas A&M University (TAES); University of Tennessee (TENN); University of Texas (TEX); University of California at Berkeley (UC); U. S. National Herbarium (US); University of South Florida (USF); Vanderbilt University (VDB); University of Vermont (VT); Naturhistorisches Museum, Vienna (W); University of Wisconsin (WIS).

Dr. Robert K. Godfrey, of the Tall Timbers Research Station, helped by sharing his observations about andropogons. I wish to thank Bob and his wife, Nell, for making a home for my wife and me for many days. Thanks are also due to Mr. and Mrs. Angus K. Gholson, Jr., of Chattahoochie, Florida, and to Dr. and Mrs. Walter S. Judd, of Gainesville, Florida, for their hospitality. Angus and Walt pointed out many good collecting sites.

The six months of field work in the southeastern United States was funded by the Anderson and Fernald funds of Harvard University and by the National Science Foundation (Dissertation Improvement Grant number DEB-77-17317).

The skill and diligence of my brother Philip are reflected in the photographic plates. Finally, for her assistance in the field, support at home, and perseverance through the years, I thank my wife, Pegze.

LITERATURE CITED

ALLARD, R. W. 1975. The mating system and microevolution. Genetics **79:** 115–126.

BAZZAZ, F. A. 1975. Plant species diversity in old-field successional ecosystems in southern Illinois. Ecology **56:** 485–488.

BOOTH, W. E. 1964. Agrostology. 222 pp. Edwards Brothers, Ann Arbor, Michigan.

BROWN, W. V. 1949. A cytological study of cleistogamous *Stipa leucotricha.* Madroño **10:** 97–107.

———. 1950. A cytological study of some Texas Gramineae. Bull. Torrey Bot. Club **77:** 63–76.

CAMPBELL, C. S. 1980. Biosystematic studies in the *Andropogon virginicus* complex (Gramineae). 217 pp. Unpubl. Ph.D. thesis, Harvard University.

———. 1982a. Hybridization between *Andropogon glomeratus* var. *pumilus* and *A. longiberbis* (Gramineae) in central Florida. Brittonia **34:** 146–150.

———. 1982b. Cleistogamy in *Andropogon* (Gramineae). Am. Jour. Bot. **69:** 1625–1635.

———. 1983. Wind dispersal of some North American species of *Andropogon* (Gramineae). Rhodora **85:** 65–72.

CARNAHAN, H. L., & H. D. HILL. 1961. Cytology and genetics of forage grasses. Bot. Rev. **27:** 1–162.

CELARIER, R. P. 1956. Cytotaxonomy of the Andropogoneae I. Subtribes Dimeriinae and Saccharinae. Cytologia **21:** 272–291.
———. 1957. Cytotaxonomy of the Andropogoneae II. Subtribes Ischaeminae, Rottboelliinae, and the Maydeae. *Ibid.* **22:** 160–183.
———. 1958. Cytotaxonomy of the Andropogoneae III. Subtribe Sorgheae. *Ibid.* **23:** 395–418.
———. 1959. Cytotaxonomy of the Andropogoneae IV. Subtribe Sorgheae. *Ibid.* **24:** 285–303.
CHAPMAN, R. H., & S. B. JONES. 1975. Ecotypic differentiation in *Andropogon virginicus* (Gramineae). Bull. Torrey Bot. Club **102:** 166–171.
CHASE, A. 1937. Notes on types of North American grasses. Am. Jour. Bot. **24:** 33–35.
——— & C. D. NILES. 1962. Index to grass species. 3 vols. 1743 pp. G. K. Hall, Boston.
CHAUDRA, N., & N. SAXENA. 1964. Morphological studies in the Gramineae 5. Vascular anatomy of the spike and spikelets of the Andropogoneae. Proc. Indian Acad. Sci. B. **59:** 457–474.
CHURCH, G. L. 1936. Cytological studies in the Gramineae. Am. Jour. Bot. **23:** 12–15.
———. 1940. Cytotaxonomic studies in the Gramineae. *Ibid.* **27:** 263–271.
CLAYTON, W. D. 1964. Studies in the Gramineae: V. New species of *Andropogon.* Kew Bull. **17:** 465–470.
———. 1967. *Andropogon pterophilis* Hook. Ic. Pl. **37:** *t. 3644.*
———. 1969. A revision of the genus *Hyparrhenia.* Kew Bull. Add. Ser. **2:** 1–196.
———. 1972. Studies in the Gramineae: XXXI. The awned genera of Andropogoneae. Kew Bull. **27:** 457–474.
CLIFFORD, H. T. 1961. Floral evolution in the family Gramineae. Evolution **15:** 455–460.
CONNOR, H. E. 1979. Breeding systems in grasses: a survey. New Zealand Jour. Bot. **17:** 547–574.
COTTON, R., & C. A. STACE. 1977. Morphological and anatomical variation of *Vulpia* (Gramineae). Bot. Not. **130:** 173–187.
DAVIDSE, G., & R. W. POHL. 1972. Chromosome number, meiotic behavior, and notes on some grasses from Central America and the West Indies. Canad. Jour. Bot. **50:** 1441–1452.
DUJARDIN, M. 1978. Chromosome numbers of some tropical African grasses from western Zaire. Canad. Jour. Bot. **56:** 2138–2152.
FERNALD, M. L., & L. GRISCOM. 1935. Three days of botanizing in southeastern Virginia. Rhodora **37:** 129–157, 167–189.
GOLLEY, F. B. 1965. Structure and function of an old-field broomsedge community. Ecol. Monogr. **35:** 113–137.
GOULD, F. W. 1956. Chromosome counts and cytotaxonomic notes on grasses of the tribe Andropogoneae. Am. Jour. Bot. **43:** 395–404.
———. 1967. The grass genus *Andropogon* in the United States. Brittonia **19:** 70–76.
——— & T. R. SODERSTROM. 1970. Chromosome numbers of some Mexican and Colombian grasses. Canad. Jour. Bot. **48:** 1633–1639.
GOULD, S. J. 1977. Ontogeny and phylogeny. 501 pp. Belknap Press, Harvard University, Cambridge, Massachusetts.
GRAHAM, A. 1973. History of the arborescent temperate element in the northern Latin American biota. Pp. 301–314 *in* A. GRAHAM, ed., Vegetation and vegetational history in northern Latin America. Elsevier Publ. Co., New York.
GUTTIERREZ, M., V. E. GRACEN, & G. E. EDWARDS. 1974. Biochemical and cytological relationships in C_4 plants. Planta **119:** 279–300.
HACKEL, E. 1889. Andropogoneae. *In:* A. L. P. P. DE CANDOLLE & C. DE CANDOLLE, Monogr. Phanerog. **6:** 1–716.

HARTLEY, W. 1950. The global distribution of the tribes of the Gramineae in relation to historical and environmental factors. Austral. Jour. Agr. Res. **1:** 355–373.

———. 1958. Studies on the origin, evolution, and distribution of the Gramineae. I. The tribe Andropogoneae. Austral. Jour. Bot. **6:** 115–128.

HESLOP-HARRISON, J. 1961. The function of the glume pit and the control of cleistogamy in *Bothriochloa decipiens* (Hack.) C. E. Hubbard. Phytomorphology **11:** 378–383.

HITCHCOCK, A. S. 1951. Manual of the grasses of the United States. ed. 2 (revised by A. CHASE). 1054 pp. U. S. Dept. Agr. Misc. Publ. **200.**

HOLMGREN, P. K., & W. KEUKEN. 1974. Index herbariorum. Part I. The herbaria of the world. Reg. Veg. **92:** 1–397.

KANNENBERG, L. W., & R. W. ALLARD. 1967. Population studies in predominantly self-pollinated species. VIII. Genetic variability in the *Festuca microstachys* complex. Evolution **21:** 227–240.

KEEVER, C. 1950. Causes of succession on old fields of the Piedmont, North Carolina. Ecol. Monogr. **20:** 229–250.

KENG, Y. L. 1939. The gross morphology of the Andropogoneae. Sinensia **10:** 274–343.

KRAL, R. 1976. Additions to some notes on the flora of the southern states, particularly Alabama and middle Tennessee. Rhodora **78:** 438–456.

LAESSLE, A. M. 1958. The origin and successional relationships of sand-hill vegetation and sand-pine scrub. Ecol. Monogr. **28:** 361–387.

LELONG, M. G. 1965. Studies on the reproduction and variation in some *Panicum* subgen. *Dichanthelium*. 226 pp. Unpubl. Ph.D. thesis, Iowa State University.

LINNAEUS, C. 1753. Species plantarum. Ray Society facsimile of the first ed. 2 vols. 1200 pp. B. Quaritch, London. 1957, 1959.

LONG, R. W., & O. LAKELA. 1971. A flora of tropical Florida. 962 pp. Univ. Miami Press, Coral Gables.

MABRY, T. J., K. R. MARKHAM, & M. B. THOMAS. 1970. The systematic identification of flavonoids. 354 pp. Springer-Verlag, New York.

METCALFE, C. R. 1960. Anatomy of the monocotyledons. I. Gramineae. 731 pp. Clarendon Press, Oxford.

MOHLENBROCK, R. H. 1973. The illustrated flora of Illinois. Grasses. *Panicum* to *Danthonia*. 378 pp. Southern Illinois Univ. Press, Carbondale, Illinois.

MURRAY, B. G. 1974. Breeding systems and floral biology in the genus *Briza*. Heredity **33:** 285–292.

NASH, G. V. 1903. Poaceae. Pp. 60–65 *in* J. K. SMALL, Flora of the southeastern United States. Published by the author, New York.

PARODI, L. R. 1949. Las gramíneas sudamericanas del género *Deschampsia*. Darwiniana **8:** 415–475.

POHL, R. W. 1978. How to know the grasses. ed. 3. 200 pp. Wm. C. Brown Co., Dubuque, Iowa.

——— & G. DAVIDSE. 1971. Chromosome numbers of Costa Rican grasses. Brittonia **23:** 293–324.

RADFORD, A. E., H. E. AHLES, & C. R. BELL. 1964. Manual of the vascular flora of the Carolinas. 1183 pp. Univ. North Carolina Press, Chapel Hill.

ROBERTY, G. 1960. Monographie systématique des Andropogoneae du globe. Boissiera **9:** 1–455.

SCRIBNER, F. L. 1901. The grasses in Elliott's "Sketch of the botany of South Carolina and Georgia." U. S. D. A. Div. Agrost. Circ. **29:** 1–12.

SMITH, C. E., JR. 1962. Henry Muhlenberg—botanical pioneer. Proc. Am. Philos. Soc. **106:** 443–460.

STAPF, O. 1919. Gramineae. *In:* D. PRAIN, ed., Fl. Trop. Africa **9:** 208–265.

STEBBINS, G. L. 1957. Self-fertilization and population variability in higher plants. Am. Nat. **91:** 337–354.

———. 1974. Flowering plants. Evolution above the species level. 379 pp. Belknap Press, Harvard University, Cambridge.

TATEOKA, T. 1962. A cytological study of some Mexican grasses. Bull. Torrey Bot. Club **89**: 77–82.

TOMPSETT, P. B. 1976. Factors affecting the flowering of *Andropogon gayanus* Kunth. Responses to photoperiod and growth regulators. Ann. Bot. **40**: 695–705.

WEATHERBY, C. A. 1942. A list of type specimens in Elliott's herbarium. Rhodora **44**: 249–262.

WEATHERWAX, P. 1929. Cleistogamy in *Poa chapmaniana*. Torreya **29**: 123, 124.

WET, J. M. J. DE. 1954. Chromosome numbers of a few South African grasses. Cytologia **19**: 97–103.

———. 1960. Chromosome numbers and some morphological attributes of various South African grasses. Am. Jour. Bot. **47**: 44–49.

APPENDIX A. **Glossary**.

CALLUS—the very base of the spikelet, covered with hairs in all members of the virginicus complex (FIGURES 1, 2, 8, and 9).

COLLAR—the region of the leaf at the junction of the blade and the sheath.

DISPERSAL UNIT—the spikelet and the attached rachis internode and pedicel (FIGURES 1, 2, 8, and 9).

INFLORESCENCE—the portion of the stem producing reproductive structures.

INFLORESCENCE UNIT—the racemes, the peduncle, and the subtending raceme sheath (FIGURE 11).

LIGULE—a membranaceous flange on the adaxial surface of the leaf at the collar (FIGURE 4).

PEDICEL—a short axis attached at its base to the rachis internode and with or without a vestigial spikelet (FIGURE 8).

PEDICELED SPIKELET—the spikelet at the apex of the pedicel; nonfunctional and reduced or absent in the virginicus complex (FIGURE 8).

PEDUNCLE—the axis subtended by the raceme sheath and bearing at its apex two or more racemes (FIGURE 11).

RACEME—the linear series of spikelets connected by the rachis internodes (FIGURE 11). "Rame," designating a structure with sessile and pediceled spikelets, has been used in *Andropogon* (Pohl, 1978).

RACHIS INTERNODE—the axis connecting the spikelets into racemes (FIGURE 8).

APPENDIX B. **Rules for determining distance between character states.***

I. For characters of type a ((low range) mean (high range); characters 1, 7, 8, 9, 29, and 31), type b (low range–high range; characters 10, 26, and 27), and type c ((low range) low mean–high mean (high range); characters 19, 20, 23, and 25), compare the ranges of types a and b and the intervals between the low and high means of type c, then assign a value based on the following conditions:
   - 0, if the range of each overlaps more than half the range of the other, or the range of one is totally contained within the range of the other.
   - ½, if the range of one is less than or equal to half the range of the other.
   - 1, if the range of each overlaps that of the other by less than half.

II. For characters with two or three states (characters 2, 3, 5, 6, 11, 13, 18, 24, 28, 30, and 32):
   - 0, if identical for all states.
   - ½, if different in one or more but not all states.
   - 1, if no states are shared.

*See TABLES 4–6.

III. For the two pubescence characters (4 and 17):
 0, if identical in half or more of their states but different in less than two.
 ½, if identical in less than half of their states and different in two or or more.
 1, if no states are shared.

IV. For character 12:
 0, if identical in all states.
 ½, if identical in some states but different in others.
 1, if not identical in any states.

V. For character 14:
 0, if overlap is half the total range or more.
 ½, if overlap is less than half the total range, or if 1–2 vs. 2–3 or 2–3 vs. 3–4.
 1, if no overlap, or if 1–2 vs. 2–5 or 2–3 vs. 3–5.

VI. For character 15:
 0, if overlap is half the total range or more, or if the range of one lies entirely within the range of the other.
 ½, if overlap is less than half but more than 0 or if endpoints of two ranges are equal (e.g., 1–2 vs. 2–3, 2–4, 2–5, or 2–6; 2–3 vs. 3–5).
 1, if no overlap, or 2–3 vs. 3–7, 11.

VII. For character 16:
 0, if the mean of each falls within the range of the other.
 ½, if the mean of one lies outside the range of the other.
 1, if the mean of each lies outside the range of the other.

VIII. For character 22 there are three classes: A is 2 (3 or 4); B is 2–3, 2–4, or 2–5(–7); and C is 2–9 or 2–13. Distance is based on the following conditions:
 0, if classes are identical.
 ½, if class A vs. B.
 1, if class A or B vs. C.

IX. For character 21, there are three classes: A, if range of means is less than 10 (e.g., (2)4–6(12)); B, if range of means includes 10 (e.g., (1)6–14(60)); and C, if range of means is greater than 10 (e.g., (9)26–66(15)). Distance is based on the following conditions:
 0, if classes are identical.
 ½, if class A vs. B or B vs. C.
 1, if class A vs. C.

X. For character 33, there are three classes: A, mean less than 10%; B, mean 10–50%; and C, mean greater than 50%. Distance is based on the following conditions:
 0, if classes are identical.
 ½, if class A vs. B or B vs. C.
 1, if class A vs. C.

APPENDIX C. **Ambiguous names.**

Andropogon belvsii Desv. Opusc. Sci. Phys. Nat. 67. 1831. Type: no locality cited; this name based on an unnamed figure (*t. 23, fig. 4*) of Palisot de Beauvois, Essai Nouv. Agrost. 1812. Although Jackson (Index Kew. **1:** 124. 1893) equated this with *Andropogon argyreus* Schultes, and Hitchcock (1951) equated it with *Andropogon ternarius* Michaux, the illustration alone is not enough to determine the placement of this name.

Andropogon louisianae Steudel, Synopsis Pl. Glum. **1:** 383. 1854. The description ("spica solitaria") does not fit the *Andropogon virginicus* complex. Although Chase (1937) said the type of this name (P) is a "small, over-mature plant of *A. virginicus*," in Hitchcock (1951) the name was doubtfully referred to *A. virginicus* L.

Andropogon virginicus L. subvar. *ditior* Hackel in DC. Monogr. Phanerog. **6:** 411. 1889. Types: Florida, Duval County, *A. H. Curtiss 3639d* (Curtiss distributed three species under this number: *Andropogon glomeratus* (Walter) B.S.P. var. *pumilus* Vasey, the